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CONTENTS

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THE BOTANICAL REVIEW

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ORIGIN AND DEVELOPMENT OF PRIMARY VASCULAR TISSUES IN SEED PLANTS

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INTRODUCTION

Current concepts of the origin of primary vascular tissues and interpretations of different stages in development of these tissues are much confused and are becoming more so through uncritical adoption in literature of new ideas introduced by some of the more speculative writers. Furthermore, certain important topics of vascular ontogeny, as, for example, direction of differentiation of procambium and phloem in primary organs, development of vascular connections between main and lateral axes, vascularization of

embryos and seedlings, and transition from primary to secondary growth, have never been thoroughly investigated. This review is an outcome of the writer's efforts to prepare a basis for studies leading to better understanding of the origin and development of primary vascular tissues and to clarification of the ontogenetic relations of and developmental and structural differences between primary and secondary vascular tissues. It reexamines the data which workers have used in formulating their concepts of vascular differentiation and reevaluates the terminology that has been and is being developed in the literature on vascular ontogeny.

ORIGIN OF THE VASCULAR MERISTEM IN VEGETATIVE SHOOT APICES OF ANGIOSPERMS AND GYMNOSPERMS

Term and concept of procambium. The meristem which gives rise to primary vascular tissues is commonly termed "procambium" in distinction from the "cambium" that produces secondary xylem and phloem. Early botanists applied the word "cambium" to all meristems, that is, to apical meristems as well as to procambium and cambium (see 138). According to Hanstein (93), for example, the formative tissue which appeared as a roundish mound—the "punctum vegetationis"—at the apex of a shoot and as strands below the apex constituted the cambium. He distinguished between apical meristem and meristematic strands by terming the former "apical cambium" ("Gipfelcambium", also "cambium terminale") and the latter "formative strands" ("Bildungsstränge", also "fasciculi cambiales"). Other early workers (116, 168, 174) referred to these strands simply as "cambium bundles" ("Cambiumbündel"). After some vascular tissues differentiated from these cambial strands, an interfascicular formative tissue ("Zwischen-Bildungsgewebe", also "cambium interfasciculare", (93) united the bundles into a continuous ring, as seen in transverse sections. Thus, the formative tissue of the bundles and the interfascicular cambium together produced a complete formative ring, or a "cambial cylinder" ("Bildungsring" or "tubus cambiales", (93).

Nägeli[1] was opposed to application of the term "cambium" to all meristems because the latter were not all alike. Principally two types of "Theilungsgewebe" existed in the plant body. One of these,

[1] Every author mentioned in this paper is cited in the bibliography. Therefore, citation numbers are given only when there is more than one citation for an author.

which Nägeli named "meristem", was parenchymatous in nature, divided by walls perpendicular to the long axes of the cells, and showed no apical growth in individual cells. The other, "cambium", was composed of elongated, prosenchymatous cells which divided mostly parallel to their long axes and pushed their ends among each other by growth at their apices. At first, the entire plant organ consisted of meristem; later, only apical portions of stems and roots remained meristematic. The extreme apex constituted the "Urmeristem" ("promeristem") which, although not entirely homogeneous, showed no indications of tissue segregation. Below it were the partially differentiated meristems, the "Folgemeristeme" and the cambium. The latter appeared as strands of elongated cells imbedded in the "Folgemeristem" tissue. The cambium bundles and the meristematic areas appearing between the bundles together constituted the "cambium ring" in Nägeli's nomenclature. He stated, however, that "cambium-meristem-ring" would have been a more appropriate term for this structure. The interfascicular regions could become converted into cambium, or some of the fascicular cambium could transform itself into meristem and produce rays. Thus, Nägeli sharply distinguished between meristem and cambium on the basis of cell shape, cambium in his concept being composed of elongated or prosenchymatous cells, meristem of short or parenchymatous cells; on the other hand, he did not clearly separate the cambium ring that produced secondary vascular tissues from the earlier ring-like structure composed of cambium bundles and meristematic interfascicular areas.

In contrast to Nägeli, Sanio (168) restricted the term "cambium ring" to the meristem producing secondary vascular tissues, but at the same time applied "cambium" not only to prosenchymatous (fusiform initials) but also to parenchymatous (ray initials) cells of the cambium ring. In other words, the "cambium" of the "cambium ring" of Sanio received its modern definition. It was not yet, however, separated from the earlier stage of development of the vascular meristem, the procambial stage, since Sanio continued to employ the term "cambium bundle".

Sachs (165, 166) finally suggested replacing "cambium bundles" with the term "procambium" and reserving "cambium" for the meristem that produced secondary xylem and secondary phloem.

Russow (163) criticised the term "procambium" because, he said,

it implied that the tissue was a precursor of the cambium, whereas actually it developed into the different tissues of the vascular bundles, including the cambium. Russow, therefore, introduced the term "desmogen" to replace "procambium", but this term was not generally adopted and "procambium" became firmly implanted in botanical literature.

As was mentioned above, the terms "meristem" and "cambium" were distinctly separated in Nägeli's nomenclature. Later workers, however, began to apply the term "meristem" not only to parenchymatous meristems, but to procambium and cambium as well. The latter two became the special kinds of meristems producing vascular tissues. Russow (163), for example, used "meristem" in this enlarged sense, and through De Bary (18, 19) the broad definition of the term became well established.

In modern morphological works (*e.g.*, 10, 79), the vascular meristem, when first evident, is often designated as "provascular tissue" or "provascular meristem". These terms have a more general meaning than "procambium" and are particularly convenient if one has no further interest in vascular differentiation than in locating its beginnings. Whether they are more appropriate than "procambium" in a consideration of later stages of primary vascular differentiation and particularly of cambium development at the beginning of secondary growth, may, however, be questioned.

The present writer favors retention of the term "procambium" but at the same time recognizes the necessity for revising the concept covered by this term. The objection to "procambium" raised by Russow that the term places the tissue in relation to the cambium only, is not serious. Procambium is related to primary vascular tissues as cambium is to the secondary. The cambium produces not only phloem and xylem but more cambium as well, and, similarly, procambium gives rise to xylem and phloem and may have some additional meristematic cells which eventually assume the characteristics of the cambium of mature plant organs. "Procambium" and "cambium" denote two developmental stages of the same vascular meristem which produces xylem and phloem and perpetuates itself at the same time. The procambial meristem may fail to form cambium by being used up in the production of primary vascular tissues; this occurs generally in vascular cryptogams and in extreme herbaceous dicotyledons, and is characteristic of mono-

cotyledons. Other aspects of the relation between procambium and cambium will be considered in a later section of this paper.

Haberlandt gave a very broad definition to "procambium", including under this term not only the meristem that produced primary vascular tissues but also all other prosenchymatous meristematic cells in the primary body. This definition has not been generally accepted, however, and "procambium" has come to mean specifically the vascular meristem from which primary xylem and phloem are derived. The present writer approves of this specific use of the term "procambium" but recognizes that further developmental studies are required to give a proper ontogenetic interpretation of the prosenchymatous and sclerenchymatous sheaths, caps and layers on the periphery of the phloem which are usually classified as pericyclic tissues. As will be shown in the section on the pericycle, this tissue frequently arises in such close association with primary phloem—and also with xylem, if the sheath completely surrounds the bundle—that both pericycle and primary vascular tissues appear to be derived from the same meristematic region.

The usual definitions of "procambium" (*e.g.*, 102) stress such characteristics of procambial cells as relative length, narrow transverse diameters, and density of protoplasts. The shape of the cells is a result of repeated longitudinal divisions, combined with growth in length but accompanied by little transverse growth. One should remember, however, that the characteristics of procambial cells change during development of the meristem. In particular, the length of cells increases many times and the density of cytoplasm decreases until the procambium appears as highly vacuolated as the cambium.

The relative length which procambial cells attain before their transformation into vascular elements varies in relation to the stage of vascular differentiation and also to the position in the plant body. The earliest phloem and xylem elements are shorter than those maturing later. Procambial cells in leaves and flowers may remain short. In roots the meristematic cells which eventually differentiate into vessels are very wide, and in monocotyledons they may even have larger transverse than longitudinal diameters. The concept of procambium must be sufficiently broad to take into account morphological variability of the meristematic cells that develop into primary vascular elements.

Relation of procambium to apical meristem. Some of the early botanists held that the procambium arose as discrete strands directly from the general meristem at the apex; others found, immediately below the apex of the shoot, a ring-like zone of undifferentiated cells within which the procambium subsequently differentiated. The most important proponent of the former view was Nägeli who believed that, almost without exception, development of the "cambium ring" began with the appearance of the "cambial strands" which arose from the "Urmeristem". Others (116, 140, 174) distinguished, beneath the apex of a stem, a ring-like zone of "cambial tissue" which separated pith from cortex and gave rise to vascular bundles and intervening parenchyma tissue. "Cambium ring" and "thickening ring" ("Verdickungsring") were the terms applied to this annular zone, as well as to the cambium that produced the secondary vascular tissues.

The picture of the origin of the vascular meristem was further developed by still others (27, 118, 168). According to these workers, a meristematic zone between apical meristem and procambium was characteristic of all groups of phanerogams. Sanio (168) suggested reserving the term "thickening ring" for the region that preceded the procambium and using "cambium ring" only for the meristem that produced secondary xylem and phloem. He justified the term "thickening ring" on the basis that the region to which it referred showed active divisions, particularly tangential, which contributed to the thickening of the primary axis. Koch (118) pointed out that the "Verdickungsring" was not a new meristem but a remainder of embryonic tissue present from the beginning at the apex of the shoot. Above, this tissue predominated; below, it was reduced to a ring-like zone through the appearance of pith and cortex. Bouygues (27) referred to this meristem as "méristème prévasculaire" to distinguish it from the "méristème générale" at the apex.

Active longitudinal divisions in certain areas of the meristematic ring initiated the procambium bundles. At first, these structures appeared united with each other because they differed so little from the ring tissue remaining between them. Later, the bundles became distinct from the interfascicular tissue. In plants with secondary growth the interfascicular tissue apparently retained embryonic characteristics, as it later gave rise to the interfascicular cambium (118).

In gymnosperms (118) the pith matured early but the cortex and the thickening ring remained alike so that the latter constituted the inner part of a peripheral meristematic zone. In plants with a solid vascular core, as in certain aquatics, the cortex became parenchymatized early, leaving a solid core of "prevascular meristem" (27). Sometimes the procambial divisions occurred so close to the apex that the ring-like area became delimited after the procambial bundles were initiated (118, 168). Therefore, according to Koch, in some plants the existence of a ring could be questioned: procambial strands appeared to arise as discrete units from the apical meristem. Koch implied that failure to recognize variations in the relative time of appearance of the procambium was involved in the old dispute regarding the origin of this meristem.

De Bary (18, 19), who had so much influence upon the formulation of concepts in anatomy, did not clear the matter regarding the origin of the procambium. He simply stated that vascular bundles arose in an annular zone characterized by active longitudinal divisions during initiation of procambial strands, and did not relate this zone to the apical meristem. He considered Sanio's ideas, but was mainly concerned with the question whether vascular bundles arose in the plerome or the periblem or both.

Whatever their views on the relation between procambium and promeristem of the apex, the early workers recognized that the first vascular strands of stem apices originated in connection with leaf primordia and constituted prolongations of the main vascular bundles of the leaves (116, 93, 94, 144, 140, 168, 118). It is beyond the scope of this review to consider the problem of relation between leaf traces and the vascular system of the axis, but for the sake of clarity the present writer's viewpoint on this matter should be indicated. Throughout the present review the primary vascular system of phanerogams is treated as a system which is made up of leaf-trace material. In many instances the reported cauline or stem bundles may be interpreted as compound structures related to more than one trace; in other words, as "sympodial" structures. The morphologic nature of cauline bundles that seemingly cannot be so interpreted remains to be determined. (See 115). Use of the term "leaf trace" should also be clarified at this point. This term is employed to designate each bundle which extends to a leaf.

Despite certain work (168, 118, 27), Nägeli's concept that iso-

lated strands arose directly below the apex and were subsequently united into a continuous vascular cylinder, prevailed in botanical literature and was carried over into the most recent texts (63, 180). This interpretation, however, did not remain unchallenged. Kostytschew (120, 121), after examining about 130 species of dicotyledons, concluded that procambium bundles rarely arose as discrete strands, and that when they did, no continuous ring of xylem and phloem, primary or secondary, was produced. Unfortunately this worker did not clearly distinguish between the meristematic zone that preceded the procambium and the procambium proper. The "procambium ring", a term which he used instead of "thickening ring", sometimes referred to Sanio's (168) "Verdickungsring", sometimes to an older region. His methods were not suitable for study of the earliest stages (he removed the protoplasts from the sections), and, therefore, his discussion largely referred to regions where procambial differentiation had progressed considerably. The picture that subsequent workers obtained from Kostytschew's study was well illustrated in Priestley's (153) statement that in the vast majority of dicotyledons the procambial elements arose below the apex as a continuous ring, subsequent isolation of bundles occurring through development of parenchymatous tissue from parts of the procambium ring. Similarly, Carstens reported a continuous procambium ring in a large number of gymnosperms and woody dicotyledons.

Thus the picture of the origin of procambium became rather more confused than before. Formerly there were two schemes: discrete strands from primordial meristems *vs.* discrete strands from a remainder of the primordial meristem. Now a new interpretation has been added: from the primordial meristem arose the "procambium ring" which later could be broken up into individual strands. Several recent workers undertook, therefore, a reexamination of the problem.

In contrast to Kostytschew (120, 121) and Carstens, who were particularly concerned with the relation of procambium to secondary growth, others (102, 105, 134, 114, 115) devoted their entire attention to the phenomena preceding procambial differentiation. Helm (102) reinvestigated several plants previously used by Kostytschew (120, 121), employing modern methods of microtechnic. In addition to the paraffin method he tested vital dyes and indicators on

fresh sections and found that in treatment with H_2O_2, bubbles arose from regions that were differentiating into pith and cortex but that none was formed in sections of apical meristem, of procambial strands and of the ring-like zone above the procambium. Helm (102) doubted that this test indicated distribution of catalase in the tissues because, obviously, bubbles were absent from regions that were most meristematic. At the same time he was unable to prove that occurrence of bubbles over the primordial pith and cortex was related to the possible presence of intercellular spaces in these regions.

In all plants investigated—some were of the type that, according to Kostytschew (120, 121), had discrete procambium strands, others a procambium ring—Helm (102) found a ring of meristematic cells that preceded procambium formation. The cells composing this ring were similar to those of the apical meristem in size, shape, staining properties and reaction to H_2O_2. Sometimes the ring was clearly differentiated from the future pith and cortex; or special staining and vital tests had to be applied for its recognition. Relative prominence of the ring depended on the degree of differentiation in adjacent tissues. Because of the cytological similarity between the ring and the apical meristem, Helm (102) emphasized that the ring constituted no new tissue but was a remainder ("Rest") of the apical meristem and that his term "primary meristem ring" ("primärer Meristemring") or simply "meristem ring" was to be used for denoting a topographical concept only. The ring had, of course, the shape of a hollow cylinder in a tri-dimensional aspect.

According to Helm (102), the meristem ring appeared above the youngest node. Where leaf traces, in their basipetal differentiation from leaves, came in contact with the ring, the cells of the latter divided to form the downward axial continuation of the procambium of the traces. Above the connection between leaf trace and ring, parenchyma differentiated in the ring and thus a leaf gap was produced. If the traces were relatively small, certain areas of the ring did not differentiate into procambium and the latter appeared in the form of isolated strands. In plants with large traces, uniting into a continuous cylinder in the primary body, the entire ring was converted into procambium. Thus Helm attempted to reconcile the opposing views of his predecessors by distinguishing between the primary meristem ring and the procambium ring and by indicating the relation of procambium bundles to the two structures.

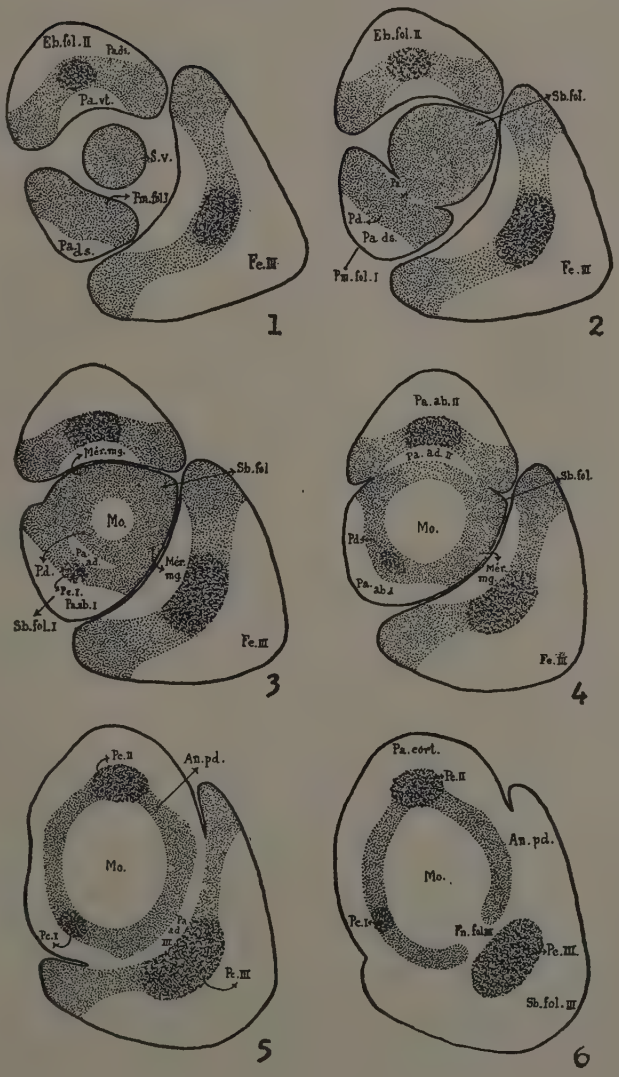
Helm's (102) concept was used and also further developed by several other investigators (17, 134, 62, 172, 114, 115, 84).

Like many workers before him (94, 144, 168, 118), Helm (102) recognized that procambial differentiation in the axis and development of leaves were interrelated. But, in Helm's concept, the blocking out of the meristem ring was apparently independent of leaf formation. In contrast, Louis emphasized the idea that the region set aside for procambial development was delimited only in relation to leaf differentiation (Figs. 1–7). Following Grégoire's (86) suggestion, Louis substituted the term "prodesmogen" for the "primary meristem ring" of Helm, to indicate that within the ring arose the desmogen, or procambium. Blocking out of the prodesmogen occurred through parenchymatous differentiation of pith and cortex (Fig. 5). Although parenchymatization of the pith could occur very close to the summit of the bud—even above the youngest node—no parenchymatization ever took place in the peripheral region of the axis above the axillary pocket of the youngest leaf primordium (Fig. 3). Thus, unlike Helm, Louis found no meristematic ring above the youngest node (Figs. 1 and 2). (Louis used only serial paraffin sections and did not attempt to apply vital tests, as were employed by Helm.)

According to Louis, parenchymatization of stem cortex occurs in conjunction with the same process in foliar primordia. Within the latter the dorsal (primordium I in Fig. 1) and, somewhat later, the ventral parenchymatization (foliar protuberance II in Fig. 1) block out a prodesmogenic arc continuous with the "marginal meristem"[2]

[2] Louis uses the term "marginal meristem" in a different sense than other students of leaf development. Commonly "marginal meristem" is employed to designate the marginal ridges of meristem which appear on both sides of the midrib region and produce the lamina of a leaf primordium (75). Louis, speaking of the marginal meristem, refers to the peripheral meristematic region of the axis which occurs above the level of cortical parenchymatization (Figs. 3 and 4).

FIGS. 1–6 (After Louis, 1935). Diagrams of successive transverse sections through the shoot apex of *Arabis alpina*, figure 1 showing the highest, figure 6 the lowest level. The stippled areas are more meristematic than the blank areas. Undulate markings indicate procambial areas. The abbreviations are: *An.pd.*, prodesmogenic ring; *Eb.fol.*, foliar protuberance; *Fe.*, leaf; *Fn.fol.*, leaf gap; *Mér.mg.*, marginal meristem; *Mo.*, pith; *Pa.*, parenchyma; *pa*, meristem beginning to parenchymatize; *Pa.ab.*, abaxial parenchyma; *Pa.ad.*, adaxial parenchyma; *Pa.cort.*, cortical parenchyma; *Pa.ds.*, dorsal parenchyma; *Pa.vt.*, ventral parenchyma; *Pc.*, procambium; *Pd.*, prodesmogen; *Pm.fol.*, foliar primordium; *S.v.*, vegetative apex; *Sb.fol.*, foliar buttress; *Sg.*, segment of the axis.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Pe.II
An.pd.
Mo.
Pe.I
Pa.fol.III
Pe.III
Sb.fol.III
6

of the young axis above (Figs. 3 and 4). [illegible] differentiation occurs in the foliar protuberance as well as in its buttress ([illegible] in Fig. 7). The buttresses form the peripheral part of the axis because they overtopped the latter. Therefore, parenchymatization of the buttresses delimits the prodesmogen of the axis. (Follow line [illegible] through sections in Figs. 1–3.)

Depending on the [illegible] of the axial prodesmogen occurs at different levels. In [illegible] the prodesmogen is delimited in the [illegible] because of a completely overtopping [illegible]; in [illegible] and [illegible] in the second; in [illegible] in the third mode. [illegible] in that [illegible] parenchymatization of [illegible] and buttresses occurs very late so that the prodesmogen constitutes the outer portion of a peripheral meristematic region. In front of the adaxial [illegible] of the buttress the prodesmogen may become parenchymatous and thus continuity is established between cortical and medullary parenchyma (Fig. 8).

Louis' work is particularly important because it elucidates the problem of "interdependence" between leaf and stem in the building up of the vascular system. The prodesmogen of the leaf and the stem [illegible] at which the leaf is attached is delimited as a unit. The prodesmogen of the buttress belongs to the leaf primordium and at the same time is part of the prodesmogen of the stem segment. There is thus no question of a "union" of systems of leaf and stem, nor of a "building" of leaf traces.

Unfortunately Louis' paper does not include a consideration of procambial differentiation, and the resulting emphasis on prodesmogen creates the impression that the building up of the tissues is a very distinct phase clearly separated from procambialization.

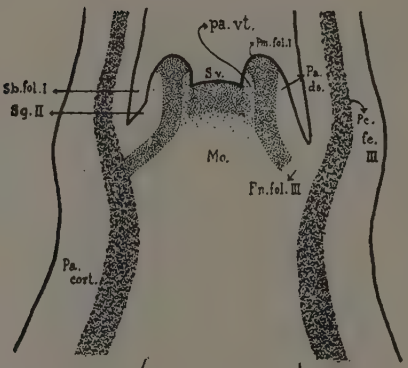
[illegible] illustrations of leaf histogenesis, however, suggest [illegible] early appearance of procambium in leaf primordia. Some of them ([illegible]) show that before the leaf forms a [illegible] the first [illegible] [illegible] longitudinal divisions and elongation of cells mark the initiation of procambium beneath the emerging primordium. The interpretation of these elongated cells as procambium and not as prodesmogen is [illegible] with Louis' terminology because in his own words "the prodesmogen is [illegible] with the general [illegible]." [illegible] procambial differentiation [illegible] to the [illegible]

layer of cells from the apex in *Vinca minor* (cells marked with crosses in the corpus in Fig. 8). If this interpretation is correct, identification of prodesmogen in such an apex seems highly problematical.

Louis' figure 20, here reproduced as Figure 7, shows prodesmogen in the two youngest leaves; however, the photomicrograph in Louis' paper (Plate 3, Fig. 21 *bis*), representing an enlarged view of the same leaves, suggests that the "prodesmogen" is composed of elongated cells and merits interpretation as procambium. In the foliar primordia of *Carya Buckleyi*, Foster (73) pictures procambium beneath a barely elevated leaf protuberance, while in a primordium comparable in size to the youngest leaves in figure 7 he shows the procambium strand reaching to the meristematic apex of the primordium (Fig. 9). Unlike Foster and the other students of foliar histogenesis, Louis did not follow leaf development cell after cell and used conspicuousness of vacuolation as the main basis for distinguishing between different meristematic regions.

Thus the usefulness of Louis' classification of vascular meristem in shoot apices into prodesmogen and procambium may be seriously questioned. Prodesmogen as a term is also open to criticism. As Helm (102) points out, "prodesmogen" implies that the meristem is destined to become vascular tissue, whereas in plants with discrete vascular bundles in the mature body, part of the "prodesmogen" differentiates into parenchyma of the "medullary rays". Then Helm remarks that designation of the region by a specific new term suggests that something new has appeared, whereas "prodesmogen" is supposed to be a remainder of the general meristem. In the present writer's opinion, "prodesmogen" is inappropriate also because the term "desmogen" is seldom used and the combination "prodesmogen" and "procambium" is incongruous.

Helm's (102) concept and term of "meristem ring" also has its serious weaknesses. The proximity of procambial differentiation to the apex, as indicated by works on foliar histogenesis, suggests the possibility that Helm's "meristem ring" is not homogeneous at its first appearance, but is composed of procambial strands and some less specialized cells in the interfascicular regions. Furthermore, the "ring" varies greatly in its distinctness in different kinds of plants. In gymnosperms and small-leaved angiosperms (118, 17, 134, 114, 115) the procambium differentiates in a peripheral region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Pn. fol. I
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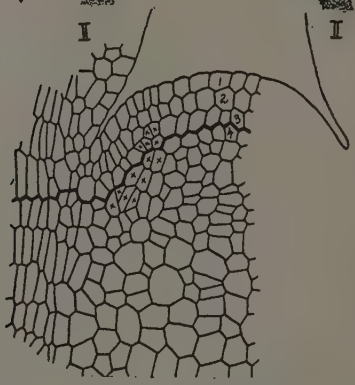
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pc

9

("Periphermeristem", (115)) which apparently is not yet separated into cortex and meristem ring. In certain other plants the meristem preceding procambium appears as a solid core ("Meristempfropf", (115)) which undergoes procambization only in its peripheral part (late medullation, according to Kaplan (115)) or in its entirety. It remains to be determined whether any vital test will give a different picture and reveal the ring-like zone before it is delimited by increasing vacuolation of the adjacent parts. As Kaplan (115) points out, the processes considered in these studies occur in an extremely short zone of the shoot apex so that preparation of sections for vital studies is most difficult. Kaplan attempted to study polarization phenomena of cell walls in paraffin sections, but did not obtain conclusive data. In general, he observed that pith cells tended to show double refraction first, the meristem ring last, the latter sometimes only at the beginning of differentiation of the first vascular elements from the procambium. He connected this behavior with the prolonged meristematic condition of meristems concerned with vascularization.

Helm (102) goes beyond introducing the term and concept of "meristem ring." He offers a complete set of terms—a substitution for Hanstein's (95) "plerome", "periblem" and "dermatogen" —in which the "meristem ring" occupies equal rank with three other primary meristems, the "dermatogen" (precursor of epidermis), "phleoegen" (precursor of cortex) and "metrogen" (precursor of pith). These terms are hardly more useful than those of Hanstein, because they also carry specificity and determination of tissues too close to the apex and do not take into account the ability of the pith and cortical regions to produce vascular bundles (leaf traces in cortex, intraxylary bundles in pith, cortical sieve tubes in Cucurbitaceae, cortical and medullary bundles in certain Cactaceae, *etc.*).

Kaplan (114, 115) further developed the principal ideas of Helm and Louis and applied them to the formulation of his concept of the stele. Like his predecessors, he overstressed the distinctness and

FIG. 7 (After Louis, 1935). Longitudinal section of a shoot apex of *Syringa vulgaris*. Stippling indicates the general meristem and prodesmogen, undulate markings the procambium. Abbreviations as in figures 1–6. FIG. 8 (After Schmidt, 1924). Median longitudinal section of a shoot apex of *Vinca minor*. Crosses mark the youngest procambial cells. FIG. 9 (After Foster, 1935*b*). Median longitudinal section of a leaf primordium 93.6 microns high of *Carya Buckleyi*. Details are *c*, abaxial cortex; *pc*, procambium. The heavy lines in figures 8 and 9 separate the tunica, above, from the corpus, below.

extent of the zone preceding the procambium. However, the term employed by Kaplan for this zone, "residual meristem" ("Restmeristem"),[3] is less specific than "prodesmogen" and "meristem ring". "Residual meristem" is applicable to all meristematic areas below the apex in which parenchymatization has been delayed, namely, the future vascular region, apical and marginal meristems of leaves, primordia of axillary buds, and sometimes also cortex and pith, if these are late in appearance. The residual meristem of the axis can appear in the form of a meristem ring, as a peripheral meristem or as a meristematic core. In anomalous dicotyledons and in certain monocotyledons the residual meristem, according to Kaplan (115), forms several rings concentrically arranged.

When Kaplan (114, 115) states that residual meristem is a continuation of apical meristem he recognizes the variability and complexity in cytological make-up of apices in different groups of plants. (See in this connection the recent review on apical meristems by Foster (78).) In some plants the initial zone of the apical meristem, the promeristem ("Urmeristem"), is not "typically" meristematic; its cells have longer diameters and more prominent vacuoles than the cells derived from it. The "typical" densely cytoplasmic and rather small meristematic cells constitute the "eumeristem" in Kaplan's (115) terminology and the residual meristem is eumeristematic in nature. The eumeristem may begin at the apex and continue into the residual-meristem region (many angiosperms); or it may begin below the apical initials (many pteridophytes); or it may be first represented in the residual meristem, the apex being conspicuously vacuolated (*Psilotum, Selaginella*). Use of the term "residual meristem" in the latter case seems incongruous; the remainder is very different from the whole, at least cytologically.

Kaplan (115) speculates on the degree of similarity between residual meristem and promeristem. He favors the idea that residual meristem is still as totipotent as promeristem and that differences appear later when certain areas of residual meristem differentiate into procambium.

Thus Helm (102, 105), Louis and Kaplan (114, 115) agree that

[3] In English a translation of "Restmeristem" into "rest meristem" would be ambiguous because "rest" means not only "remainder" or "residue" but also "repose". A more appropriate translation seems to be "residual meristem" which is here adopted.

that vascular system of shoots arises not directly from the promeristem of the apex but in a region located slightly lower, a region which is as highly meristematic as the promeristem and which becomes delimited as such through increased vacuolation of pith and cortex or cortex alone. Within this region the procambium strands differentiate in relation to the leaf primordia. The work of these authors has, no doubt, added much to the understanding of the phenomena involved in the blocking out of the vascular system; however, the value of interpolating a special distinct phase between apical meristem and procambium is yet to be tested by means of detailed histogenetic studies.

The investigations of Helm, Louis, Kaplan and of the workers who supported their concepts have thus far remained largely separated from researches on shoot apices and foliar histogenesis, like those of Schmidt, Foster, Cross and others. The two lines of approach to studies on tissue origin in vegetative shoots must be correlated before the phenomena of procambial development are clearly understood. As already indicated, a comparison of the picture produced by Helm, Louis, and Kaplan with results of studies on foliar histogenesis reveals the striking difference in estimation of distances from the apex to the first procambial divisions by the investigators of the two groups. A closer examination of studies on foliar origin is, therefore, pertinent.

Modern studies on development of leaves deal with angiosperms and relate the phenomena involved in leaf initiation to the structure and activity of the apical meristem. The botanists of the past century were largely concerned with the question whether vascular bundles arose in the plerome or periblem (18, 19); present-day workers consider the role of tunica and corpus[4] in the formation of procambium.

The tunica and corpus of different plants vary both in their relative thickness and in the degree of participation in leaf development. In wheat (161) only one tunica layer is present and the leaf with its procambium develops from this layer. Periclinal divisions, apparently concerned with initiation of the procambium of the trace, occur, however, in the corpus. In dicotyledons the tunica frequently consists of more than one layer. According to Schmidt, in *Vinca minor* the tunica is three-layered. During leaf initiation periclinal

[4] Regarding the structure of shoot apices, see reviews by Foster (77, 78).

divisions, producing elongated cells, occur in the outermost layer of the corpus and also in the tunica (Fig. 8). Schmidt thinks that the divisions in the corpus probably begin procambial differentiation in the internode. They are in progress when the apex is in the minimal-area stage, that is, at the very beginning of a new plastochrome. Cross and Johnson (57), studying *Vinca rosea,* found similar early initiation of procambium ("provascular tissue"). In *Hypericum uralum* (215), the tangential divisions initiating the vascular bundle in the third and fourth tunica layers, along with some similar divisions in the second tunica layer, are instrumental in producing the first visible protuberance of the emerging leaf primordium.

Foster (73) shows that the leaves and scales of *Carya Buckleyi* arise in the two-layered tunica and the outer region of the corpus, the procambium of the traces in the corpus. Foster observes the procambium at a somewhat later stage than Schmidt and Zimmerman, namely, at the base of primordia 50–90 microns high. In somewhat larger foliar organs of *Carya,* 90–190 microns high, the procambium reaches the meristematic apex of scales and leaves (Fig. 9), that is, as indicated before, it extends also through the region that Louis (134) regards as prodesmogen.

Cross (53, 54) reported procambium in *Morus alba* at the base of a leaf primordium less than 75 microns long; the scales, however, first showed procambium when they were 750–900 microns long. In the phyllodes of *Acacia,* according to Boke (23), the procambium of the median bundle appeared at the base of the primordium shortly after the latter was initiated, and probably most of the procambium of the stem and phyllode base came from the corpus.

This review of studies on the origin of procambium shows that there is considerable uncertainty in literature regarding identification of the youngest procambium cells. The limits between primordial meristem cells at the apex and procambium cells below are vague and are placed at different levels by different workers. It is, obviously, difficult to identify the first divisions preparing the vascular meristem because periclinal divisions are not limited to the future vascular regions and because transformation of the relatively non-specialized meristem into procambium is very gradual. In the writer's opinion, however, minute histologic studies on large amounts of material should make it possible to determine whether

the early tangential divisions beneath emerging leaves are, in a given species, related to procambial development. If such a relationship exists, the cells resulting from the divisions might well be named simply "procambium" and not "provascular tissue", "prodesmogen" or "desmogen". It seems superfluous to apply different terms to the successive and intergrading stages of the differentiating vascular meristem of the primary body, or to give different names to the same tissue. If it seems necessary to indicate specially the undifferentiated cells preceding the procambium or those located between the youngest procambium bundles, the term "residual meristem" appears most appropriate.

Thus far this review has been concerned with longitudinal transition from apical meristem to procambium. The problem of lateral growth of procambium also merits consideration. Workers seem to agree that procambium increases in thickness gradually through divisions of the original procambial cells as well as through addition on its periphery of new cells from adjacent less specialized regions (196, 63, 73, 74, 65, 66; and others). Since these additions occur at increasing distances from the apex, the cells that become procambial at lower levels are somewhat larger and more conspicuously vacuolated than the first cells that initiate the procambium. In the words of De Bary (19), "The initial strands (procambium) arise from and consist of initial cells, of successively different degree and value. . . ." If the leaf has several traces the smaller ones may be initiated in more conspicuously vacuolated cells than the earlier appearing traces. Foster (73, 74) describes the cells differentiating into the lateral scale traces in *Carya* as somewhat vacuolated cells. Thus cells that are converted into procambium at lower levels of the axis are not unchanged promeristem cells (as those of the "meristem ring", "prodesmogen" or "residual meristem" of Helm, Louis, and Kaplan, respectively), but are partly differentiated parenchyma cells. The parenchymatous nature of cells producing vascular bundles is particularly strikingly illustrated in plants with intraxylary vascular tissues, where even the parenchyma of the protoxylem may develop phloem strands (14, 66). Obviously, from the histogenetic viewpoint, the limits between vascular tissues and adjacent parenchymatous regions are vague in both longitudinal and transverse directions. As Jost (112) has said, the location within the plant body is more important in determining the ultimate

specialization of cells than their initiation in a certain area of the meristem.

Direction of procambial development in shoot apices. Two methods of procambial differentiation have been described in botanical literature. In one, the procambium first appears at the leaf base (or in the leaf proper) and from here develops in two directions, upward into the elongating leaf primordium and downward into the axis until it meets and unites with older leaf traces (like the xylem in Fig. 12). In the other, the procambium of a new leaf primordium differentiates acropetally from the axis into the leaf in continuity with the older procambium (like the phloem in Fig. 12).

References to both methods of differentiation may be traced to the earliest works on ontogeny, but in many of these the first appearance of vascular bundles is not clearly separated from the first differentiation of xylem. Only few investigators definitely specified when they meant initiation of bundles as contrasted with maturation of vascular elements. Suffice it here to refer to De Bary (19) for a review of the earliest papers on this subject. A perusal of literature since De Bary shows that workers have not yet obtained a clear picture of the course of development of procambium in shoot apices, and, indeed, have not devoted much attention to the problem. Many recent papers refer to basipetal differentiation of axial procambium as though the workers assume this to be the usual course. Perhaps the method of xylem differentiation, which normally follows a basipetal path in the leaf trace, is taken as an indication of similar behavior of procambium and phloem.

According to Herrig, divisions at the base of *Elodea* and *Galium* leaves initiate the procambium which eventually connects the leaf veins with bundles in the stem. Lange states that the divisions which prepare for vascular differentiation at the base of leaves in *Solanum* are propagated basipetally. The leaves of *Bryophyllum* in which procambium appears and develops basipetally are 60–70 microns high, according to Yarbrough. Langdon reports downward differentiation of procambium of leaf traces in *Quercus* and *Carya* seedlings.

Flot studied the development of leaf primordia in numerous dicotyledons and obtained the general picture that vascular meristem was initiated before foliar primordia emerged and that it differentiated basipetally, branching above the axillary bud of a

lower leaf. The bundles of the youngest leaves appeared more distinct nearer the apex than farther down—another proof of basipetal differentiation, according to Flot.

Foster (73, 74) reports basipetal differentiation in traces of foliar organs in *Carya,* Cross (53, 54) in traces of leaves and scales of *Morus.* In *Viburnum,* according to Cross (55), "differentiation of the provascular tissue proceeds acropetally and basipetally in the usual manner". Brooks mentions appearance of the median procambial strand in the almond leaf 90 microns high and its subsequent basipetal differentiation in the stem axis.

Procambial course was similarly interpreted in monocotyledons, as by Bugnon (30) in the Gramineae and by Guillaud in other monocotyledons. Because procambial strands were gradually built up through addition of cells on the periphery, Guillaud thought the earliest course of procambial development could be judged by the thickness of the strands. He found the leaf traces to be thickest in or below the leaf bases and concluded that differentiation was basipetal. Attempting to interpret the specific differences in the length of apices in the Gramineae, Sharman assumed that provascular strands were initiated in the primordia and later "linked up" with the system lower in the stem.

In Helm's (102) concept of early vascularization the downward differentiation of leaf-trace procambium is one of the basic assumptions: formation of the leaf gap through parenchymatization of part of the meristem ring and procambization of other parts of this ring occur after the leaf trace in its downward differentiation approaches the meristem ring. Barthelmess, in his studies on Coniferae, and Gráf, in reference to *Bidens,* treat the problem similarly to Helm (102), except that Gráf thinks the leaf gaps are formed not because a trace approaches the ring, but because the meristem of the ring fails to receive here a stimulus for vascularization from above. Gráf assumes some material substance which, flowing from the differentiating leaves, induces procambial differentiation. Hasselberg, studying herbarium and alcohol-preserved material of Loganiaceae, reports basipetal trace development without furnishing any specific evidence.

Like Helm, Kaplan (115) makes basipetal differentiation of leaf traces one of the important premises in the development of his concept of vascularization of the primary plant body.

The idea of basipetal differentiation of leaf-trace procambium has been ascribed to Louis by several workers (23, 24, 75, 77, 96). As already indicated, Louis omitted consideration of procambium from his studies on prodesmogen, but, in regard to the latter tissue, he strongly emphasized its original unity in stem and leaf. In addition, he stated that the prodesmogens of two superposed nodes were continuous from their inception, the connection being established through the marginal meristems. (Observe in Figures 3 and 4 the marginal meristem,[3] *Mér.mg.*, connecting the prodesmogens of primordium 1 and of the foliar buttress, *St.fol.*—the buttress of the next primordium to emerge—to the right, above.) It is instructive to quote Louis regarding his view on the unity of prodesmogens and his reference to procambium:

"De ces observations, nous avons pu conclure qu'au stade fondamental de la morphogénèse conductrice, il n'y a pas lieu de parler de 'raccordement.' La continuité existe d'un niveau a l'autre dès le début et par suite de la formation même du prodesmogène.

"Nouse ne considérons pas, dans ce travail, le phenomène de la procambisation ni le raccordement des procambiums.

"Ce que nous venons de dire ne concerne, il est bon d'y insister, que le 'raccordement' *fondamental* des structures conductrices, c'est-a-dire le raccordement des meristèmes prodesmogeniques. Une étude complète du raccordement conducteur comporterait l'observation de l'étape suivante, celle des cloisonnements procambiaux: mais nous avons dit que cette seconde etape des phenomènes sort du cadre de la présente étude".

Since Louis has so strongly emphasized the idea that prodesmogen formation is a primary phase, distinct from the secondary phase of procambialization, he might have held the view that the procambium followed a different course than the prodesmogen. In his discussion concerning vascularization of shoots of *Lonicera periclymenum* he inferred that the trace procambium differentiated basipetally. This species of *Lonicera* has three traces to each leaf. Where the vascular bundles occur in a ring within the axis the traces of different leaves alternate. This intermingling of bundles belonging to different leaves seems to conflict with the notion that leaf buttresses constitute distinct entities. Louis, however, explains that the concept of leaf buttresses has reference to delimitation of

[3] See footnote 2.

the prodesmogen only. Within the latter the traces of a given leaf may prolong themselves *from a higher buttress into a lower* so that they alternate with the traces of the lower leaf. There is no "interpenetration" of buttresses.

One might also surmise that Louis stood for the idea of downward differentiation of trace procambium, from treatment of the problem by Grégoire (87), under whose guidance Louis produced his work on prodesmogen. Grégoire was very certain that procambium developed basipetally in the stem, so that, in phanerogams, the vascular system of the shoot is composed of leaf traces united into a sympodial system: "Aussi on on ne voit jamais, dans un axe feuillé, les faisceaux constituer des cordons *continus* de bas en haut, d'où se détacherait, aux noeuds, des cordons latéraux destinés aux feuilles; toujours, d'une manierè ou d'une autre, le système conducteur de l'axe est *sympodial*". To support his contention, Grégoire cites others (31, 128, 122, 152, 17, 115, 96, 84, 141). In the opinion of the present writer, none of these workers has produced proof of basipetal differentiation of axial procambium. In referring to the concept of prodesmogen, Grégoire states that continuity of this meristem is necessary so that the procambial strands of foliar origin may prolong themselves into the axis.

Regarding the course of procambial development, Schmidt's paper on apical meristems deserves special consideration. Although Schmidt does not exactly specify in what direction procambium differentiates, his careful analysis of cell orientation and division indicates that continuity of this tissue is evident extremely early, namely, when the primordia are just emerging. Schmidt's illustration of the apex of *Vinca minor* with the youngest procambium marked by crosses is reproduced in figure 8. The eight marked cells in the corpus are the first cells of the procambium strand (leaf trace) of the youngest internode, the five marked cells in the innermost layer of the tunica are the initial procambial cells of the leaf. Thus, according to Schmidt, the procambium of the internode and of the leaf is initiated as one continuous structure. The further question is whether the procambium of one internode is always continuous with the procambium of another, lower internode. Schmidt reports such continuity only when the pith begins to be parenchymatized and the procambial cells of the youngest internode assume the characteristic elongated shape.

Koch (118) mentioned acropetal differentiation of procambium in gymnosperms. Tangential divisions and cell elongation occurred in the inner derivatives of the peripheral stem region from the point of connection of these derivatives with the tissues of the lower internodes and thence basifugally towards the leaf primordia.

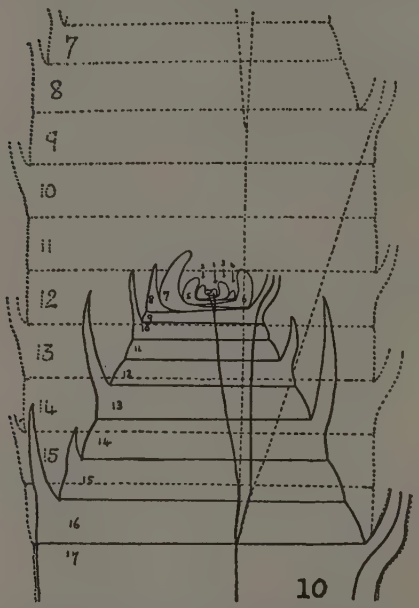


FIG. 10 (After Priestley, Scott, and Gillett, 1935). Diagram of a shoot of *Alstroemeria* showing the position of connections of median strands in the orthostichy 1, 9, and 17. The diagram also shows the effect of extension of the internodes on these connections. FIG. 11 (From Strasburger, *et al.*, 1919, p. 84, fig. 116). Diagram of a monocotyledonous axis showing the course of the vascular strands which appear exposed in a median section. The leaves *Aa*, *Bb*, and *Cc* have been cut off near their bases. The strands ending at the large letters *A*, *B*, and *C* are median traces, those ending at the small letters *a*, *b*, and *c* are lateral traces. Above, the stem appears in a transverse section.

Koch (119) also reported upward differentiation of procambium in dicotyledons, from the base of the internode into the leaf, but did not indicate whether at the same time this procambium was continuous with the same tissue in the lower, older internode.

Some workers (156, 155) recognized procambium in primordia

of *Alstroemeria* that were less than 50 microns long and they pictured this procambium as differentiating acropetally through 16 internodes from the point of connection with the trace of an older leaf to the base of the new primordium. Figure 10 illustrates the interpretation given by these workers. Sixteen internodes below the attachment of leaf 1, its trace is connected with the trace of leaf 9 located on the same orthostichy as leaf 1 but attached eight internodes lower. From the point of its origin the trace to leaf 1 continues in the axis upward through 16 internodes, then bends off into leaf 1. Eight internodes below the insertion of leaf 1 its trace is connected with a younger trace which is differentiating acropetally toward a primordium that is to emerge eight internodes above leaf 1. According to the concept of Priestley and his co-workers, the trace to leaf 1 originated from the trace to leaf 9 when the latter was the youngest primordium; similarly, the new trace branching off from trace 1 arose when leaf 1 was the youngest primordium. Figure 10 also shows the effect of axis elongation upon the connections between the different traces of the orthostichy 1–9–17.

The procambium of veins within the leaf proper showed varied differentiation in *Alstroemeria* (156). The first five main procambial strands and two subsidiary ones developed acropetally, other longitudinal bundles differentiated basipetally.

Recently, Crafts (51) reported in an abstract that procambium in a *Sequoia* shoot differentiated acropetally in continuity with the older traces in lower internodes.

Majumdar speaks of an "entirely basifugal desmogen differentiation" in the shoot apex of *Heracleum* but supports his statement only by showing the continuous procambium strand in a fairly large primordium (140 microns high) and does not consider procambial differentiation during the initial stages of primordium formation.

References to basifugal differentiation of leaf-trace procambium are beginning to appear in current papers on apical meristems and foliar histogenesis. According to Boke (23) in phyllodes of *Acacia:* "from the time that procambium cells may first be detected in the phyllode base by means of their prosenchymatous form and deeper staining qualities, they form a continuous chain, traceable into the stem where they anastomose with the adjacent lateral trace of an older phyllode". In *Trichocereus spachianus* (Cactaceae), Boke (24) reported the occurrence of cauline bundles as well as of

leaf traces, and observed continuous acropetal differentiation of procambium in both types of strands. Another representative of the Cactaceae, *Opuntia cylindrica,* showed the same continuous acropetal development of procambial strands, but none of the latter was cauline.

In contrast to his earlier observations on *Morus* and *Viburnum,* Cross (56, 57) reports acropetal differentiation of provascular tissue in *Vinca rosea* and *Cunninghamia lanceolata;* at least the development is acropetal within a given internode, the strand differentiating from the internode into the leaf. The initial continuity with vascular tissues of the older stem parts, however, has not been demonstrated with certainty. It is true that in *Vinca,* a plant with opposite leaves, the provascular strand to a given leaf is said (57) to be continuous from the beginning in the two internodes and the intervening node[6] immediately below, but figure 9 shows that the continuity of this strand is at first interrupted at the intervening node. Only somewhat later the two superposed strands "become continuous" (*57, 628*).

Satina and Blakeslee did not specifically investigate procambial differentiation in *Datura* shoot apices, but reported that the cells of the third layer which gave rise to procambial cells formed a continuous strand in very young leaf primordia.

Regarding the course of procambium in shoot apices, Helm's (103) study on the effect of removal of leaves from shoot apices seems particularly significant. Using *Lysimachia punctata* and *Ricinus communis* in many replications, Helm, with careful technic, removed leaf primordia at their earliest stages of emergence. The treated plants were left to develop for some time and were then sampled for microscopic study. Helm found that removal of young primordia considerably affected development of the procambium of leaf traces. Near the former location of the primordium the trace consisted of somewhat elongated cells, parenchymatous in appearance and even enclosing intercellular spaces. Farther below, within the ring of bundles, the affected trace had a nearly normal appearance of a procambial bundle except for the smaller diameter as compared with the traces of unmutilated leaves. Helm concluded that only that part of a trace was affected which was in the process

[6] In the paper (*57, 633*) "intervening internode" has been erroneously used instead of "intervening node".

of differentiation when the leaf was removed, that is, the upper part of the trace. The lower part was already differentiated and was not materially affected. To the present writer these experiments suggest acropetal differentiation of procambium, but Helm does not make this deduction.

Thus, according to the present review, many workers have reported that procambium was initiated at the base of the leaf primordia and thence differentiated acropetally into the primordia and basipetally into the stem. These authors, however, have largely failed to give convincing evidence in support of their conclusions. On the other hand, some very recent investigations on leaf ontogeny report continuous and acropetal differentiation of procambium.

Further studies on initial stages of procambization are pertinent. In the writer's opinion such investigations should follow, first of all, the methods of approach used by students on the origin of leaves because, apparently preparation of the vascular meristem occurs at the very apex before the emergence of leaves. In her own observations on dicotyledonous apices the present writer has thus far been unable to observe discontinuity of procambium. However, one should not discount the possibility of variable behavior in relation to specific differences between plants, to differences in type of structures, and to variation in growing conditions.

COURSE OF DIFFERENTIATION OF THE FIRST VASCULAR ELEMENTS IN VEGETATIVE SHOOTS OF ANGIOSPERMS AND GYMNOSPERMS

Course of the first xylem. De Bary (19) reviewed the oldest investigations pertaining to the origin and direction of differentiation of the first xylem and phloem in shoots. Briefly, workers reported, as with respect to procambium, an intimate relation between leaf development and the origin of vascular tissues of the axis. Some, however, found that vascular elements developed acropetally from the stem into the leaf in continuity with older traces in the axis, others reported that vascular tissues appeared first in isolated strands at or near the base of the leaf and then differentiated in two opposite directions, acropetally into the leaf, and basipetally through the axis. (See vessel development in Fig. 12.) Sometimes the basal portion of the trace differentiated acropetally in continuity with the mature xylem of the axis, the other portion basipetally from the leaf, the two parts meeting and uniting in the axis.

Although in discussing differentiation of vascular bundles De Bary (18) spoke of "Ausbildung" ("Completion" (19)) of bundles, meaning maturation of vascular tissues in general, the early workers usually considered xylem only. The phloem either was not mentioned or was assumed to follow the same course as the xylem. Moreover, as already noted, workers did not always distinguish between the first appearance of procambium and maturation of tissues from it. De Bary (19) stated that the two processes, initiation of procambium and differentiation of vascular tissues, could follow different courses in the same bundle. Nevertheless, references in De Bary's text to the origin and differentiation of vascular tissues in shoot apices may be taken as largely concerning the xylem.

After De Bary (19), workers continued to study xylem differentiation, mentioning phloem only occasionally. Basipetal differentiation of trace xylem was reported in monocotyledons by Guillaud; in *Melaleuca* by Lignier. According to Weiss, in certain dicotyledons with internal phloem, xylem differentiation in the axis was usually basipetal, sometimes acropetal. Lanessan described acropetal differentiation in *Syringa,* basipetal differentiation from the very apex of the leaf in certain other species. Col studied several dicotyledons, found basipetal diminution in thickness of leaf traces, and concluded that dfferentiation of the latter followed a downward course.

Trécul (201–204, 206, 208) paid particular attention to xylem differentiation in leaves, especially in the leaf blade proper. Differentiation of the leaf blade as a whole or of leaflets of compound leaves followed varied courses. Some matured first at the base, others at the apex; in still others some parts differentiated basipetally, other basifugally. Accordingly, secondary venation showed varied patterns of differentiation. In the median vein, however, the first xylem elements usually appeared first beneath the leaf in the stem or in the lower part of the leaf and then differentiated in two opposite directions. Elements of a given bundle could arise in two places at once and then differentiate toward each other and also in opposite directions. In compound leaves of *Aesculus* (206), the xylem elements originated separately in each leaflet, then fused in the petiole and differentiated downward. In *Pavia* (206) the first xylem had double origin as some elements arose in the leaflets, others in the petiole, then grew toward each other and in opposite

directions. In axillary shoots of *Primula* (204) the pattern of differentiation was influenced by the vigor of the shoots. In most vigorous ones vessel differentiation began in the leaf and continued down into the stem; in less vigorous shoots one vessel developed downward, another was initiated at the insertion of the shoot and differentiated toward the leaf; finally, in the weakest shoots all differentiation progressed from shoot insertion toward the leaf. In the Compositae Trécul (208) found seasonal variations in the method of the origin of xylem. In the Gramineae and other monocotyledons (202, 203) the xylem of the median bundle ascended into the leaf from the stem and through the sheath; the xylem bundles of lower ranks differentiated downward from the leaf apex while their basal portions differentiated upward within the sheath.

Differentiation of xylem in the leaf blade of a monocotyledon, *Tradescantia,* has been followed in considerable detail (182). The protoxylem of the primary veins differentiates acropetally within the leaf. The median vein develops in advance of the laterals and when it reaches the apex of the leaf a terminal group of tracheids is formed there. From this group xylem strands differentiate along each margin of the leaf. This xylem follows a basipetal course until it joins that of the lateral veins differentiating acropetally. The xylem of other subsidiary veins, longitudinal and transverse, develops basipetally. The acropetal differentiation of the xylem occurs while the leaf is small and meristematic. Later, when the apex of the leaf becomes somewhat more mature than the base, the order of xylem development is reversed.

Scott and Priestley relate the differentiation of the leaf bundles to that of the vascular system of the stem. The perimedullary bundles of the internodes are continuous into the leaves as primary veins. These are the strands whose xylem differentiates acropetally from the stem into the leaf. The authors, however, do not state whether this differentiation is acropetal throughout the stem also. The basipetal xylem development which later occurs in the leaf blade is continued into the stem and results in the production of xylem strands arranged around the periphery of the internode. This xylem matures when the internode ceases to elongate, while the perimedullary and other median bundles differentiate before elongation and are ruptured by this process. As in the leaf blade, basipetal progress of the xylem in the internode occurs from a more

mature to a less differentiated region, since there is an intercalary meristem at the base of the internode. Scott and Priestley call attention to the importance of the late basipetal differentiation of the peripheral bundles in view of the usual absence of secondary growth in monocotyledons.

Thus, according to the literature just reviewed, the first xylem shows considerable variation in details of development, but its inception in isolated strands in the leaf trace or in the leaf vein and subsequent differentiation in two opposite directions appears to be a general phenomenon in angiosperms and gymnosperms. Many other investigations support this generalization (31, 122, 123, 157, 89, 156, 154, 96, 84, 66, 51).

Course of the first phloem. Some workers have reported that phloem followed, in the stem, the same basipetal course as the xylem, but they did not support their statements by convincing evidence (90, 130, 157, 96). The few attempts to study phloem differentiation in some dicotyledons in detail, by identifying individual sieve-tube elements in serial sections, have shown that, in contrast to the xylem, the phloem developed acropetally in continuity with the mature phloem in the axis (see sieve-tube development in Fig. 12; 89, 34, 66, 67). Priestley, Scott, and Gillett found evidence that in *Alstroemeria,* a monocotyledon, the phloem followed the procambium in its basifugal differentiation through the axis from its connection with the phloem of an older trace toward a new leaf primordium. (For procambium differentiation, see Fig. 10.) Within the leaf proper in some smaller veins phloem sometimes differentiated basipetally, apparently isolated from other phloem. In *Helianthus* Priestley and Scott assumed basifugal development of the protophloem system without following the course of individual elements. Indication of acropetal phloem differentiation in *Sequoia,* a gymnosperm, has been found by Crafts (51). Figure 12 gives a diagrammatic representation of the contrast between phloem and xylem in their initial course in leaf traces of a dicotyledonous shoot.

This brief review apparently covers available information on direction of development of the first phloem in shoots of angiosperms and gymnosperms. Obviously, information is very scanty. Moreover, the data supplied in each individual paper are based on small amounts of material and, excepting those of Chang and Esau (66),

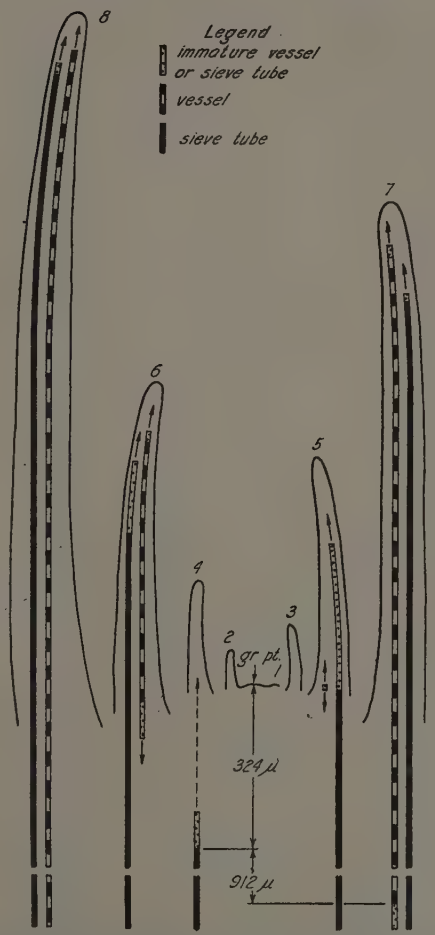


FIG. 12. Diagram of the apical region of a *Nicotiana* shoot, showing the position of the first sieve tube and the first xylem vessel in each leaf. The phyllotaxy has been disregarded, but the leaves were placed at their proper levels below the apical meristem marked *gr.pt.* (×103.) (From Hilgardia, vol. 11, no. 8.)

give little or no evidence regarding criteria used in identification of mature phloem. Chang and Esau, in following the course of individual sieve tubes, considered absence of nuclei, scarcity of stainable contents, thick walls and well differentiated sieve plates as indications of maturity of sieve-tube elements. Whatever the workers' opinion on the matter of maturity of sieve tubes (see 67), it is essential that they furnish an exact description of the elements considered in their studies so that others may have a basis for comparison. In contrast to xylem cells, sieve tubes, particularly those of the protophloem, are rather inconspicuous elements, and their developmental stages are not sharply defined. To be convincing, a report on phloem differentiation must, therefore, include precise data on the characteristics of the sieve tubes of the species considered. Regarding xylem, workers are generally agreed that elements with fully developed secondary walls and free of protoplasts are mature.

Relative time of appearance of the first phloem and xylem elements. Workers who paid careful attention to vascular differentiation and learned to recognize the first sieve tubes almost invariably have found that these elements matured before the first xylem elements of the same strand. As early as 1863 and 1864, Sanio reported that in vascular bundles of stems the phloem elements differentiated before the xylem. Later, Sanio (170) identified the phloem elements as sieve tubes in certain plants. He also found an apparent exception in *Carpinus* in which the first spiral elements of the xylem matured while active divisions were still in progress in the phloem region. Schmitz, in checking Sanio's findings, also observed sieve tubes maturing before the xylem elements. Russow (163) and Léger found early maturation of phloem elements a general characteristic of vascular plants.

According to Faber, the sieve tubes of the external phloem matured before the xylem in *Cucurbita;* those of the internal phloem differentiated almost as early. Other students of plants with internal phloem, including the Cucurbitaceae (211, 127, 13, 10, 66, 67), reported that the internal sieve tubes appeared after the xylem.

Certain papers indicate the distance from the apex to the first mature sieve tube measured in number of plastochrones. According to Chang, the first sieve tubes, with which the vascular differentiation begins, occur in the third or fourth leaf primordium in *Tropaeolum.* Griffiths and Malins reported the first protophloem

appearing in advance of the xylem in the youngest leaf rudiment in *Pisum*, in the third or fourth pairs of leaves in *Syringa, Ligustrum* and *Mentha*. Priestley, Scott, and Gillett found the first phloem in midveins of *Alstroemeria* in the fourth, xylem in the seventh leaf primordia. In tobacco (66) the first sieve tubes of the abaxial phloem appeared in the fifth or sixth primordia, the first xylem in the sixth or seventh, the first sieve tube of the internal phloem in the thirteenth.

Although sieve tubes in tobacco mature before the xylem in the leaf trace, the xylem, when once initiated, reaches the apex of the leaf before the phloem (Fig. 12; (66)). The present writer's observations indicate that other plants show a similar pattern of differentiation. This advance of xylem toward the ends of the bundles may be related to the common absence of sieve tubes in bundle ends of leaf veins. (See 67.)

Summing up the information on the pattern of differentiation of the first xylem and phloem in vegetative shoot apices, we find that in the youngest traces showing vascular differentiation the sieve tubes appear before the xylem elements. Some scanty data indicate that these sieve tubes differentiate acropetally in continuity with the mature phloem of older traces. The first xylem generally appears at the base of the leaf or in the leaf itself and thence differentiates acropetally into the primordial leaf and basipetally into the stem until it joins the mature xylem of the older traces.

VASCULARIZATION OF AXILLARY AND ADVENTITIOUS BUDS

Axillary shoots derived more or less directly from embryonic cells at the apex of the parent axis are usually distinguished from adventitious structures which arise through resumption of meristematic activity, by cells considerably removed from the apical meristem. Priestley and Swingle contrast "the further development of a meristematic shoot apex, dormant but already organized, and the initiation of such an apex as the result of developmental changes brought about by special conditions such as the isolation of a portion of a plant". This difference, however, is not fundamental (180) because various degrees of "regressive differentiation"[7] occur in the production of new shoot apices, the most extreme de-

[7] Return to a meristematic state after a more or less obvious dedifferentiation. See also discussion on regressive differentiation in the part on interfascicular cambium.

differentiation being involved in adventive shoot development during processes of regeneration from "mature" tissues. Axillary buds may remain dormant for variable periods; when they develop after prolonged dormancy, their differentiation might possibly have many features in common with that of adventitious buds.

Comparative developmental studies of shoots being organized from cell masses that had developed into tissues performing other functions than those of the meristems would be profitable in relation to the problem of vascular differentiation. In the extreme case of axillary shoots developing immediately below the main apex, the vascular connection between axillary and parent shoots differentiates in a meristematic region; in the other extreme of adventitious buds formed in connection with regeneration, the vascular connection between the bud and the axis is built through tissues that are not in a meristematic state. Is the course of vascularization influenced by the degree of specialization of cells intervening between the bud and the vascular system of the parent axis? Does the vascular connection develop from the lateral toward the main shoot or in the opposite direction? Is the direction the same under all conditions?

Unfortunately, actual data on the subject are few, especially regarding axillary buds. If the concept of basipetal procambial differentiation of leaf traces is applied to the problem of vascularization of axillary shoots, the latter may be pictured as forming their connections with the main axis by a downward differentiation of their leaf traces. Such interpretation is indeed widely accepted (157, 87, 96). However, the weakness of available evidence on direction of procambial development calls for a thorough reinvestigation of the problem.

According to Koch (119), axillary buds are not so closely related to the apical meristem as are leaves; they arise from isolated complexes of embryonic tissue derived from but not continuous with the apical meristem, so that although the first divisions occur in an embryonic region in the leaf axil, deeper cell layers, already partly differentiated, also take part in bud formation. Thus Koch would derive the vascular connection from partly differentiated cells intervening between the bud and the vascular system of the main axis. As to the direction of procambial differentiation, he says this meristem appears first in the middle region of the new axis and from here it differentiates basipetally toward the parent

axis and acropetally into the leaves of the bud. It is of interest that Koch implied acropetal differentiation of leaf-trace procambium (118) but envisioned a basipetal differentiation of branch traces (119).

In Louis' interpretation the future vascular regions of the axillary shoot and of the parent shoot constitute one unit from their inception. The parenchymatization which delimits the prodesmogen of the main axis continues into the axillary bud, so that here also a prodesmogen is blocked out in complete continuity with the prodesmogen of the main axis. Later, presumably, the procambium differentiates in the prodesmogen. (Louis does not consider this stage.) Since in Louis' concept the prodesmogen is a remnant of the general meristem of the apex, the establishment of vascular connection between the axillary bud and the main shoot through the prodesmogen would involve no other problems as that of formation of such a connection through actively meristematic cells at the apex.

Modern works on foliar histogenesis (23, 73, 161, 162, 215) indicate that the apices of axillary buds are organized in direct continuity with the apical meristem of the main axis; the authors, however, do not consider vascularization of these buds.

Studies on vascularization of adventitious shoots appear to be somewhat more numerous than those on the axillary shoots. According to Beijerinck, in buds arising on roots of *Ailanthus glandulosa* and *Aristolochia clematitis* the vascular connection between the bud and the central cylinder of the root is formed by centripetal growth of traces from the adventitious buds. He mentions xylem and phloem, but not particularly the procambial differentiation. Simon studied buds arising in callus tissue of cuttings of woody plants and agreed with Beijernick regarding the direction of development of the connecting traces. This development begins with parallel divisions in certain callus cells beneath the bud primordium. The divisions frequently spread to a few more callus cells located farther toward the interior of the callus. Still farther inward tracheids differentiate from undivided callus cells. Eventually a chain of tracheids (or vessels, sometimes) connects with the xylem of the main axis. Afterwards a meristem is formed, either in relation to the xylem strand or in continuity with the short procambium strand at the base of the bud. This meristem builds a complete vascular bundle. Differentiation of the connecting strand is not

always entirely centripetal. Meristematic strands may differentiate in the callus in centrifugal direction from the vascular cylinder of the stem. The xylem developing in these strands eventually joins the xylem differentiating in centripetal direction from the bud. Although Simon did not consider the phloem, one might draw a parallel between his description of development of the connecting strand between bud and axis with the observations of Crafts (50) on vascular union in tobacco grafts. The first connection between stock and scion was formed by sieve tubes and xylem elements differentiating directly from callus cells. Later, cambium appeared between the two lines of xylem and phloem cells and produced regular secondary vascular tissues.

Naylor has shown that in the differentiation of shoots from decapitated dandelion plants, isolated xylem appeared in the callus below the shoots, and then further xylem elements developed toward the new shoot and in the opposite direction toward the interior of the mother root.

Boodle studied development of the vascular supply for adventitious leaves of *Cyclamen* which appear near the margin of the cut surface of hypocotyl tubers borne on decapitated seedlings. Procambial tissue was formed through repeated divisions of rather large parenchyma cells in the cortex of the tuber. These divisions progressed from the adventitious buds inwards toward the vascular tissues of the tuber. He found indications of inward differentiation of xylem also.

According to Crooks, the buds regenerated upon cut seedlings of flax became connected with the primary stele of the hypocotyl by renewed cell divisions in cortical parenchyma, endodermis, pericycle, phloem parenchyma and cambium in the order named.

In their extensive studies on adventitious structures, Priestley and Swingle concluded that centripetal differentiation of the vascular connections was characteristic of both axillary and adventitious structures.

VASCULARIZATION OF FLORAL APICES

A consideration of procambial differentiation of floral apices is pertinent in this review because of Grégoire's (87) recent attempt to introduce a concept that floral and vegetative apices are fundamentally unlike in organization. The interpretation of the nature and structure of floral apices by Grégoire has been recently reviewed

by Foster (77). Only Grégoire's treatment of the problem of vascularization of these apices will be reconsidered here. As stated in a previous section, Grégoire shared the common viewpoint that the procambium of vegetative apices appeared first at the bases of leaves and then differentiated into the leaves and basipetally into the axis. In contrast, Grégoire found acropetal differentiation of procambial strands in the inflorescence, the peduncle, the receptacle, and in the floral organs. The traces, he said, did not originate in any lateral organ, neither bracteal nor floral: they developed toward these organs. Furthermore, while in the vegetative axis the descending bundles were independent at origin, in the floral ontogeny the vascular system was continuous and it sent off branches to the lateral organs. The conducting system of the vegetative shoots was of foliar origin; that of the flowers was of basal, receptacular origin, independent of the lateral organs. Grégoire interpreted the vascular system of the receptacle as simply a "reticulate mass" not related to the axial system of vegetative shoots. He even suggested abandoning the interpretation of the receptacle as an axis.

It has been sufficiently emphasized in this review that the universality of basipetal differentiation of traces in vegetative shoots, as assumed by Grégoire (87), is under serious doubt. References to acropetal development of procambium in vegetative apices appear to be on the increase in morphological papers. If the continuous acropetal differentiation should prove to be a common characteristic of the vascular meristem of shoots, one of the fundamental differences between vegetative and floral apices, as conceived by Grégoire, will be broken down.

Interestingly enough, Grégoire (87) appears to be the first to describe acropetal differentiation of floral traces as a general phenomenon. A perusal of literature on development of flowers shows that workers, if they mention the subject at all, usually report basipetal differentiation of foliar bundles. According to Grélot, the procambium of floral bracts of several species differentiated first at the base or in the free portion of the organs, then proceeded acropetally and basipetally. He was uncertain about other floral parts, but assumed descending traces in all of them. Grélot also stated that phloem differentiated before xylem, and that the first xylem formed discontinuous bundles. Trécul (205, 207) studied only xylem development in flowers of certain Cichorieae and found

the same pattern of differentiation as in leaves, the xylem appearing in isolated strands in relation to floral organs and differentiating downward in the axis. Lanessan reported basipetal differentiation of procambium and xylem in all floral organs of *Petasites, Primula* and the Rubiaceae, acropetal differentiation in *Dipsacus, Bryonia* and the Umbelliferae, and basipetal in some organs and acropetal in others in *Rivina*. According to Brooks, the procambium of a developing carpel of *Amygdalus* appeared first in the central part of the primordium and later became connected with the vascular system of the torus.

Recently Satina and Blakeslee (173) came out strongly against Grégoire's concept that the floral and vegetative apices are fundamentally different from each other. Among other things, they found indications of entirely acropetal differentiation of the procambium in both the vegetative and floral apices of *Datura*.

PROCAMBIUM AND EARLY VASCULAR DIFFERENTIATION IN ROOTS

Roots and shoots are highly dissimilar from each other in organization of their primary bodies, and the differences are evident from the beginning of development of these organs. The shoot apex produces exogenous leaf primordia, as well as the successive increments of the body of the axis; the apical meristem of the root, on the contrary, is not concerned with formation of lateral organs. This difference is reflected in the method of vascularization of the two organs. The vascular system of the shoot differentiates largely or entirely in relation to the leaf primordia, while the root develops its primary vascular body as an axial structure entirely independently from the endogenous lateral roots arising rather far below the apex. The lack of relation to lateral organs is exhibited also in the external morphology of the root which, in contrast to the shoot, is not segmented into nodes and internodes. The primary vascular tissues of the shoot are arranged in the form of more or less discrete bundles, each containing both xylem and phloem. The root has no true vascular bundles, but shows a *radial* and *alternate* arrangement of the vascular tissues. The number of protoxylem and protophloem poles is usually equal in a given root, but this number varies in different plants and in the different parts of the same root (79).

Xylem and phloem of the root arise in the central cylinder which, in the meristematic state, is often interpreted in its entirety as the

procambium because if the pith is absent, the entire central core develops into vascular tissues. Thus De Bary (19), who uses the term "initial strand" instead of "procambium", says that the axial meristematic strand is the "initial strand" of a root. Haberlandt interprets the central meristematic region as procambium. Russow (163) derives the pith of roots from the *desmogen*. Guttenberg speaks of "procambium strands" that arise mainly in the peripheral portion of the plerome. The central portion, according to Guttenberg, shows variable behavior. It may have the nature of ground meristem and develop into a pith, or it may be procambial and produce "mechanical elements". Presumably he includes conducting cells under "mechanical elements". In monocotyledons Guttenberg distinguishes between procambial cells and other "plerome rows composed of cells rapidly enlarging in all directions, having transverse walls placed perpendicularly to the longitudinal axis and possessing large round nuclei". These are the mother cells of the large vessels. Indeed, these short, wide and conspicuously vacuolated vessel mother cells do not fit the usual description of procambial elements as narrow elongated cells. They appear almost immediately behind the apical initials and, obviously, do not pass through the "typical" procambial stage. As has been pointed out in an early part of this paper, the procambium concept must be formulated with a recognition of the morphologic variability of the component elements. It is significant that Sachs (166), the originator of the term "procambium", regarded the vessel mother cells as members of the undifferentiated fibro-vascular strands which he named "procambium".

The early enlargement and loss of density of protoplasm in vessel mother cells, although particularly striking in monocotyledons, is evident also in dicotyledons and in other groups of plants (163, 109, 35, 37, 40, 189, 112, 100, 213, 91, 64, 68, 69, 150, 44). Upon maturation these cells become vessels which are usually termed "metaxylem". Despite their early enlargement and vacuolation, these elements develop their secondary walls and lose their protoplasts later than the protoxylem located near the periphery of the stele. Because of this direction of maturation, from periphery toward the interior of the central cylinder, the xylem of the roots is said to have a "centripetal differentiation". An attempt to reinterpret xylem differentiation in roots as centrifugal, on the basis of the early differentiation of metaxylem, has been made (189).

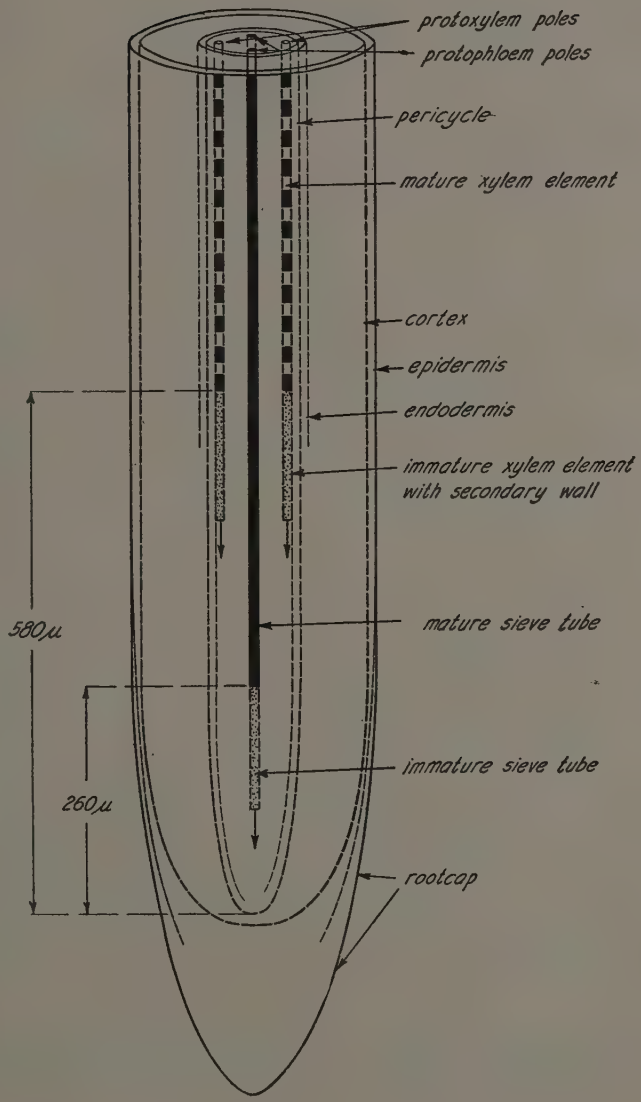
Early enlargement of metaxylem elements appears to be the result of rather sluggish cell division in this region of the central cylinder (68, 69); that is, here the meristem giving rise to primary vascular elements does not undergo numerous longitudinal divisions, as in "typical" procambium. Divisions are more frequent in the phloem region (68, 69).

The pericycle of roots may have independent initials or may arise from the same initials as the rest of the central cylinder; but in any case it early becomes a distinct continuous layer (109, 71, 68, 69). According to Guttenberg, the pericycle is not derived from the procambium of the root; Decrock (60), however, held the opposite view. At the end of primary growth the pericycle contributes some cambium to the vascular cylinder of roots having secondary growth.

The first vascular elements of roots are not always separated from the endodermis by a layer of parenchyma cells. In the Equisetaceae the first sieve tubes and vessels originate in the layer next to the endodermis (40), while in ferns only sieve tubes arise in this position. In the Gramineae and Cyperaceae the first protoxylem elements may differentiate within the pericycle (109, 35, 91). Thus the structure of roots of vascular cryptogams and of certain monocotyledons, as well as the observation that the pericycle frequently has common initials with the rest of the stele, indicates a close ontogenetic relationship between pericycle and vascular tissues of the root.

Procambium, xylem and phloem of the root apparently are always continuous with the same tissues of the basal part of the root, that is, they differentiate acropetally. In this progressive acropetal differentiation of vascular elements the sieve tubes mature closer to the apex than do the xylem elements (Fig. 13). The early differentiation of sieve tubes in angiospermous roots was recognized long ago (164, 129, 35–37) and some recent studies support these observations (64, 68, 69, 213). Nevertheless, numerous papers, old and recent, report no sieve tubes above the xylem. Elements similar in morphology and position to those that Esau (68) has described as sieve tubes in *Daucus* have been interpreted as oil ducts in certain other Umbelliferae (49, 200, 210, 100). Crooks regarded as ducts the first mature phloem elements in the *Linum*

FIG. 13. Diagram of a diarch tobacco root tip, showing spatial relations between the different regions of the root and the first vascular elements. (×130.) (From Hilgardia, vol. 13, no. 8.)


protoxylem poles
protophloem poles
pericycle
mature xylem element
cortex
epidermis
endodermis
immature xylem element
with secondary wall
mature sieve tube
immature sieve tube
rootcap
580μ
260μ

root; Hayward (99, 100) interpreted these cells as latex vessels in the *Ipomoea* root. The first phloem cells in roots of the orange were described by Hayward and Long as lysigenous ducts. The protoplasts and the end walls were said to disappear during formation of these ducts. Similarly, Chi interpreted as lysigenous cavities the first phloem cells in *Holcus sorghum* L. Only parenchyma cells were seen in the protophloem of roots of *Cucurbita* (212), in roots of *Solanum* (195). Judging by the descriptions and illustrations of the first phloem elements furnished by many of the above workers the interpretation of these elements as ducts or parenchyma may be seriously questioned.

Figure 13 shows the relative position of the first mature vascular elements in the apex of a tobacco root. The xylem may first differentiate two to several times as far from the apical initials as the first sieve tubes (69).

No recent studies are apparently available on the first phloem in roots of gymnosperms and vascular cryptogams. Early workers (164, 129, 40), however, found cryptogams comparable to angiosperms regarding early protophloem differentiation. In gymnospermous roots Russow (164) was unable to identify protophloem cells, at least he did not recognize any before or shortly after appearance of protoxylem elements. According to Chauveaud (38–41), the first phloem elements in roots and hypocotyls of gymnosperms had characters intermediate between those of the sieve tubes and parenchyma cells. He termed these "precursory elements".

Lateral roots usually arise in the pericycle or endodermis so that the bases of their central cylinders are closely proximal to the vascular elements of the parent root. Whether the xylem and phloem of the lateral root develop entirely centrifugally in constant continuity with the vascular elements of the main root has apparently not been critically investigated (19, 91). The nature of the elements connecting the vascular tissues of the two organs has been described. Cells of similar origin, as those initiating the lateral root, differentiate into short tracheal and sieve-tube elements interpolated between the vascular cylinders of the main and lateral roots (*e.g.*, 68).

VASCULARIZATION OF EMBRYOS AND SEEDLINGS

A truly complete study on the origin and development of primary vascular tissues should begin with a consideration of vascular dif-

ferentiation in embryos and continue through successive seedling stages so as to determine how the characteristic pattern of vascular ontogeny and organization is established in the primary plant body. As far as the writer is aware, there is no example of such a study in the literature on vascular anatomy. The vast literature on embryogeny deals largely with early stages of embryo development and is not particularly concerned with the manner in which the first vascular system is blocked out. The numerous papers on seedling anatomy, on the other hand, usually consider the nature of the connection between vascular systems of the root and stem of partly grown seedlings, and rarely consider any developmental aspects.

Only some exceptional papers touch upon one or another phase of early vascularization. Thus Nast has considered the first blocking out of the vascular system and the origin of the first xylem and phloem in the embryo of *Juglans*. According to this worker, vacuolation of pith and cortex in the hypocotyl-root axis of small embryos delimits the future vascular region in the form of a cylinder of densely meristematic cells. This occurs in an embryo so small that the cotyledons are not yet present as discrete structures. As the latter emerge their embryonic vascular system is blocked out by acropetal vacuolation of the ground parenchyma and this new "prodesmogen" is continuous with the previously delimited cylinder of "prodesmogen" cells in the axis below the cotyledons. The vascular meristem of the hypocotyl-root axis merges with the apical meristem at the root end of the embryo. This continuity of the two meristems suggests that the central cylinder of the future root is organized as a prolongation of the vascular meristem of the hypocotyl-root axis. Some phloem and xylem differentiate in the embryo. Within the root the former precedes the latter in time of initial appearance, but the relative time of differentiation of these elements in the embryo as a whole has not been determined. The first sieve tubes differentiate at the lower levels of the hypocotyl-root axis. The first xylem, on the other hand, is definitely related to the cotyledonary traces: it appears at the lower ends of these structures and then differentiates up into the cotyledons and downward into the root.

Dauphiné and Rivière recognized mature sieve tubes in fully developed embryos of *Lupinus*. These elements occurred throughout the hypocotyl-root axis down to the level of the root cap and ex-

tended above into the cotyledons. Sieve tubes in various stages of differentiation were also detected in *Helianthus, Ricinus* and *Mirabilis* embryos. In the first two the most differentiated sieve tubes occurred in the cotyledons. According to Phillips, the first vascular tissues of *Cynara* seedlings appeared near the base of the cotyledonary petiole and then differentiated both acropetally and basipetally. He found that in the root the phloem was defined before the xylem. Lehmberg followed the differentiation of xylem in seedlings of *Helianthus*. This tissue originated in two loci, at the base of the cotyledons and within the root, and from both of these it differentiated in two directions, the xylem of the root eventually uniting with the xylem of the cotyledonary traces. Similarly, the xylem of foliage leaves differentiated basipetally within the axis while from below other xylem differentiated acropetally from the root and the lower traces toward the higher traces. Miller reported that xylem was the first tissue to mature in *Phlox* embryos. It originated in the cotyledons, then differentiated downward and up toward the tips of the cotyledons. The sieve tubes appeared later and followed a similar course of differentiation. In the epicotyl, however, the phloem matured before the xylem and differentiated acropetally from the hypocotyl into the leaves. The xylem appeared in the leaf traces of the epicotyl and differentiated in two directions in the usual manner.

In certain gymnosperm embryos, *Keteleeria* (107) and *Cedrus* (29), xylem elements were observed in cotyledons, but no phloem was in evidence.

The above review is not presumed to be complete and is given merely to illustrate the fragmentary nature of available data on initial stages of vascular development in seed plants. The most one can suggest on the basis of these data is that the precursor of the vascular system of embryos is delimited as a unit, just as, according to Louis, the "prodesmogen" of leaf primordia and the axis is blocked out as a continuous structure in the shoot apices of seed plants. The xylem of embryos and seedlings shows the tendency to appear first in the cotyledons or their traces, but the early pattern of phloem differentiation is not yet clear.

CONCEPT OF PRIMARY AND SECONDARY VASCULAR TISSUES

Procambium contrasted with cambium. According to the common concept (63), procambium and tissues derived from it—the

primary vascular tissues—are characterized by a more or less disorderly arrangement of cells, while the cambium shows a predominance of tangential longitudinal divisions and produces cells in radial series. Yet many workers have observed that periclinal divisions frequently characterize the vascular meristem at or soon after its inception near the apex of the shoot; that the vascular tissues commonly called "primary" in stems and leaves may show radial seriation of cells. Such cambium-like behavior of the first vascular meristem or a radial arrangement of cells of the first vascular tissues have been described in all groups of vascular plants: gymnosperms (118, 168, 192), dicotyledons (2, 26, 33, 42, 60, 63, 66, 83, 92, 120, 121, 153, 154, 164, 168, 170, 191, 192, 196), monocotyledons (3, 5–9, 47, 58, 61, 82, 85, 110, 111, 158, 159, 168), vascular cryptogams (159, 160, 163). The first xylem and phloem mature before completion of the tangential divisions giving rise to the "primary" vascular tissues, so that the distance between the xylem and phloem poles gradually increases (65, 66). Thus, in contrast to a common concept (63), the procambium does not attain its full radial extent before elements begin to mature at its margins.

Orderly seriation was observed in primary xylem more frequently than in primary phloem (164, 26, 196, 121, 66). Although random cell divisions are common in that part of the procambium which gives rise to the protophloem, tangential divisions may become very prominent during formation of the metaphloem (192, 66). The origin of primary vascular tissues from an orderly dividing meristem is later frequently obscured in both xylem and phloem through differential cell enlargement, cell division and cell destruction. But unequal enlargement of cells often disturbs the radial alignment of cells in secondary xylem also. Sanio (168, 170) pointed out that primary xylem tended to show radial seriation if the tracheal elements appeared in rows alternating with rows of parenchyma (*e.g.*, tobacco (66)); but if the tracheal elements were individually dispersed among parenchyma cells, the xylem appeared as a disorderly tissue (*e.g.*, celery (65)).

Certain workers who observed radial seriation of cells in early stages of vascular ontogeny felt compelled to revise the common terminology by interpreting even the first xylem and phloem as secondary if these tissues were derived from a meristem dividing tangentially like a cambium. In many phanerogams both the so-

called "primary" and the secondary xylem arose from the same cambium-like meristem (60). Since, however, the two xylem parts differed histologically, Decrock suggested distinguishing between them by the terms "primitive" and "secondary" xylem. The procambium gave rise to the first phloem, so the latter could be termed "primary". Later Decrock (61) proposed a rigid definition of primary and secondary tissues, using presence and absence of radial seriations in meristems as a sole criterion. Similarly, a revision of nomenclature regarding vascular tissues was proposed (153, 154) based on the appearance of meristems in transverse sections. According to these authors (154): "It would seem far better to use the terms 'primary' and 'secondary' with their usual implications (the first implying origin from procambium, the second from cambium) and to recognize that in the shoot, the protophloem alone is usually primary, that the cambium arises next and the protoxylem is usually secondary, being derived from the inner members of the radial series of cells cut off from the cambium. On the other hand in roots, xylem differentiation like phloem differentiation, precedes the appearance of the cambium and both protoxylem and protophloem are primary in origin; indeed in many roots much of the earlier formed metaxylem is primary also".

The workers who stress the difference in early ontogeny of phloem and xylem (196, 154) also indicate that the meristem giving rise to xylem appears after the meristem concerned with phloem formation. In other words, the procambium first evident in the axis is the precursor of the phloem only.

Chauveaud (42) treated the problem of primary and secondary vascular tissues from a phylogenetic standpoint. He considered that the alternate (or radial) and the superposed (or collateral) arrangements of vascular tissues belonged to different evolutionary stages. The more primitive alternate arrangement occurred in the root but was omitted in the stem and leaf. In the root, superposed elements appeared after the alternate; in the stem, vascular bundles were collateral from the beginning of differentiation. In all organs, stems, leaves and roots, the superposed elements were produced by a meristem whose cells were arranged like those of a typical cambium; the alternate, on the other hand, were derived from procambium. Chauveaud, therefore, considered that superposed elements were of secondary origin and that, from the ontogenetic point of view, stems and leaves had no primary vascular tissues.

The difference between root and stem of dicotyledons, regarding cell orientation in procambium, has also been emphasized by Esau (68) : as viewed in transverse sections the procambium of the root "seems to fit the definition of the procambium better than does the corresponding vascular meristem in the stems and leaves, since in the former the walls are formed in many planes and the divisions are largely completed before the appearance of any mature vascular elements". It seems significant that according to many reports (97, 98, 136, 186, 68, 132, 101) the primary vascular tissues of the root are directly connected only with the traces of the cotyledons while the secondary xylem and phloem are continuous with vascular tissues of the plumule. But the primary vascular tissues of the plumule and the secondary of the root are produced by tangentially dividing meristems. Obviously, the various aspects of ontogeny and inter-connection of xylem and phloem of the different organs of seedlings must be considered in relation to the problem of distinguishing between primary and secondary vascular tissues.

Among workers who reported cambium-like meristem between xylem and phloem in vascular bundles of monocotyledons, some (3, 85, 158, 47, 110, 58) regarded the presence of this tissue as an indication of phylogenetic relationship between monocotyledons and dicotyledons. These two groups of plants differed only in that the cambium of monocotyledons functioned for a short time, that of dicotyledons indefinitely (58). In some species the cambium was distinct in young stages of bundle development, but the radial seriation became obscured in the differentiating tissues (3, 158). Dauphiné followed Chauveaud (42) in the interpretation of phenomena of vascularization and held that monocotyledonous roots had primary xylem and phloem, but that in the leaves the vascular tissues arose from a cambium. Andersson noted in *Lilium* that only phloem was formed by the cambium. Arber (5–8) reported intrafascicular cambium and variable amounts of secondary vascular tissues—sometimes only xylem or only phloem—in numerous monocotyledons.

Attempts of workers to introduce a rigid distinction between primary and secondary tissues based entirely upon the appearance of meristems and tissues in transverse sections has obviously confused the problem of classification of vascular tissues. Many incongruous combinations result if radial seriation of cells alone is

considered. Primary vascular tissues occur in roots but are absent from stems and leaves of the same plants. Bundles in the primary body may be composed of primary phloem and secondary xylem, or secondary phloem and primary xylem, both tissues, however, arising almost at the same time. In one family or genus the xylem of leaf traces is primary; in another the equivalent xylem—similar in position, in time of appearance, in histologic structure, and in response to elongation of the organ—is secondary. According to Priestley and his co-workers, plants may have "secondary protoxylem", "secondary metaxylem" and secondary xylem.

If the proposed nomenclature is carried a step further and all tissues exhibiting radial seriation of cells in their early ontogeny are interpreted as secondary, many parts of the primary plant body should be classified as secondary. The adaxial meristem of differentiating leaves often appears like a cambium in transverse sections (73). When the axis of many dicotyledons increases in diameter, this growth involves a succession of tangential divisions in the peripheral layers of the embryonic axis. The centripetal growth of the embryonic cortex of root tips often produces radially seriated cell layers. The calyptrogen and its derivatives frequently form continuous radial rows of cells. Orderly tangential divisions appear beneath and at the sides of the "mother cells" of apices of *Ginkgo* (76). In the embryo of *Juglans* the meristematic cylinder within which the vascular tissues differentiate increases in diameter by periclinal divisions, producing the effect of cambial activity in this region (145). These examples strongly indicate that tangential divisions are very common in the early ontogeny of the plant body and that the radial seriation in the youngest vascular meristem does not set off this meristem from other embryonic tissues of the primary body.

The originators of classification of plant tissues were aware of the frequent orderly arrangement of the first vascular tissues. It appears that the first definitions of primary and secondary tissues were conceived rather broadly, not with reference to specific morphologic characteristics, but in relation to development of the plant body as a whole. In introducing the concepts of primary and secondary tissues, Hanstein suggested that all plant parts formed from the apical meristem ("cambium" in his terminology) downward, that is, the epidermis, cortex, pith and strands of procambium

(strands of "Bildungsgewebe" in his nomenclature) constituted the young stage of the stem, the primary stem. Everything that arose from the procambium was secondary. However, a clear distinction could be made between vascular tissues formed first and those that arose later, since they differed with regard to structure and arrangement of elements, and the degree of complexity of the whole tissues. Therefore, Hanstein proposed a distinction between primary and secondary bast and wood in a special sense.

Sanio (168) noted radial seriation of cells in the procambium ("cambium bundles") and the derivative tissues. Nevertheless, he stated that cambium appeared in the cambium bundles after most cells of the later matured into wood and bast elements. Sanio termed this wood and the interfascicular parenchyma of the medullary sheath ("Markkrone") the "primary wood"; that produced by the cambium, fascicular and interfascicular, "secondary wood".

When Sachs (166) introduced the term "procambium" he did not imply that it was a tissue with disorderly arranged cells. The term had reference to the structures named "cambium bundles" by Sanio, that is, to undifferentiated vascular bundles. Both Sanio and Sachs used "cambium ring" or simply "cambium" for the meristem that gave rise to secondary xylem and phloem. Later Sachs (167) wrote that "From the very first, even before the origin of the cambium ring, the elements of the vascular bundles are arranged in radial rows".

Strasburger (191), describing the early vascularization in *Euonymus japonica* stated: "The procambium consists of thin-walled, narrow cells arranged radially"; and considering the vascular tissues of *Tilia* he wrote (192): "As in other cases, in which we studied the connection of secondary growth of bundles with the primary, a sharp limit cannot be drawn between the two in *Tilia europaea.* Tracheids, tracheae and xylem parenchyma are arranged in the primary xylem in radial rows and furthermore many rays (of the secondary xylem) are continuous with the primary-xylem parenchyma". The reference to primary growth in conifers is also significant (192): "A sharp line of demarcation between the primary and secondary parts of the vascular bundle does not exist, rather the primary merges imperceptibly with the secondary. Immediately after the elongation of shoots is completed, the first xylem ("Vasal-Primanen") and the first phloem ("Cribral-

Primanen") are crushed by elements which show a radial arrangement and are laid down in two directions by a cambial tissue. This first additional growth, which occurs in similar manner in leaf bundles, and which resembles the later additional growth in the arrangement but not in structure of elements, can be interpreted as primary. It forms here primary vessels and phloem parts in no other way, than, for example, in a monocotyledonous bundle, where such growth occurs in two directions from a meristematic layer located between the initial vascular elements ("Primanen")".

In *Tsuga* and other gymnosperms procambium strands develop within an embryonic ring-like zone through repeated periclinal divisions with omission of anticlinal divisions (118). Periclinal divisions occur in peripheral regions of the axis also before the procambium is initiated, but these divisions are followed by anticlinal ones. Koch defined the procambium merely as an embryonic tissue containing cells in various stages of differentiation into vascular elements and concerned with the production of vascular bundles.

Schoute (177), in his analysis of the concept of cambium, also stressed that primary and secondary tissues could not be clearly separated on the basis of anatomic characteristics, including radial seriation of cells. According to this worker, division into primary and secondary tissues is mainly physiological. Primary tissues are those which are derived directly from the embryo or from the "growing points". In many plants, after the organs cease to grow in length, new tissues are formed, that is, subsequent or secondary growth sets in. The role of secondary tissues, according to Schoute, is to enhance the efficiency of the already developed organs with regard to certain specific functions. Schoute says, finally: "I consider the origin (of the secondary tissues) after the termination of the growth in length as the only useful criterion for the subdivision" into primary and secondary vascular tissues. The characteristics of the meristems producing these tissues were immaterial in Schoute's concept. He used only one designation for these meristems, that of "cambium", whether the tissue originating from it was primary or secondary.

Obviously, the concept of procambium and of primary xylem and phloem as tissues with disorderly arranged cells did not originate with the creators and early exponents of these terms. Random cell arrangement does occur in primary vascular development; how-

ever, if this characteristic is included in the definition of procambium and of primary vascular tissues, the terms become very restricted. Such limited definition was actually introduced into certain general texts, but the terms themselves continued to be applied to the same structures for which they were originally designed. Chauveaud, Priestley and others attempted to eliminate this discrepancy between the definition and the use of terms by restricting application of "procambium" and "primary xylem" and "phloem" to the vascular meristem and tissues without radially seriated cells.

The present priter doubts the appropriateness of such a revision of nomenclature. A reevaluation of the present classification of vascular tissues requires for a background a thorough knowledge of the developmental phases of these tissues in all groups of vascular plants—a knowledge which at present is scanty, indeed. Procambium and cambium not only should be contrasted on the basis of appearance in transverse sections, but must be compared in radial and tangential views as well. Furthermore, the form relationships between meristematic and mature cells—for example, presence or absence of elongation in differentiating and mature cells; methods of elongation, if present; absence or presence of divisions in mother cells—may reveal sufficiently great contrasts between the tissues presently called primary and secondary that mere occurrence or lack of radial seriation of cells will appear of secondary importance.

As is well known, the cambium of arborescent species and of herbaceous dicotyledons with secondary growth displays a certain complexity of structure, caused by the presence of ray and fusiform initials. The meristem giving rise to primary tissues, on the other hand, is rather homogeneous (66). Whether other types of dicotyledons, such as vines, fleshy herbs, plants with reduced secondary growth, also show a similar difference between procambium and cambium remains to be determined. It is also pertinent to compare the procambium with the extrafascicular cambium in monocotyledons having secondary growth. Presently available information indicates that this cambium is less complex than that of dicotyledons (43).

A few scattered references to the comparative morphology of procambium and cambium of dicotyledons occur in literature. Gidon (83) pointed out that the cells of procambium were polygonal, those of the cambium rectangular, in transverse sections. He also men-

tioned that derivatives of procambium were in general individualized for some time before they differentiated into mature elements, whereas in cambium, differentiation took place close to the initiating layer. Sanio (171) and Strasburger (190) observed in the cambium a marked difference between the thick radial and the thin tangential walls, a contrast apparently not characteristic of the procambium. Others (*e.g.,* 192, 177) suggested that growth termed "secondary" began after elongation of an organ was completed. Elements differentiating during elongation differ structurally from those formed without longitudinal stretching, a feature which is particularly evident in the xylem. Sachs (166) noted the generally much elongated form of cells derived from procambium. In contrast, some cells derived from the cambium were very short. Bailey found a sudden drop in the length of tracheary elements during the change from primary to secondary growth in arborescent species of gymnosperms and dicotyledons.

As is well known, the much elongated elements of secondary tissues in gymnosperms and dicotyledons, such as fibers, become so long because of so-called "sliding growth". Such growth occurs also in secondary xylem of arborescent monocotyledons (*e.g.,* 43). Primary vascular elements apparently elongate largely, if not entirely, in conjunction with growth in length of the entire plant organ.

Among the aspects that should be considered in an attempt to distinguish between primary and secondary growth is the method of cell production, whether the latter occurs through continuous division of one row of initials ("Initialenkambium" (177)) or through division of successively new cells producing radially arranged stories of cells ("Etagenkambium" (177)). Schoute (177), in elaborating his concepts of cambia with initials and "storied" cambia, did not specifically compare procambium with cambium. He indicated, however, that all primary vascular tissues of dicotyledons may largely be produced by "true cambia", that is, cambia with initials. Even monocotyledonous bundles may be formed from such cambia. On the other hand, in some plants—species of *Vitis, Ruta, Echium, Juglans* and *Oxybaphus*—Schoute observed that the "Initialenkambium" was preceded by an "Etagenkambium". The problem obviously needs further investigation.

This review indicates that, along with similarities, the procam-

bium and cambium, in the old sense of these terms, display certain fundamental differences in structure and method of tissue formation. But it also reveals the conspicuous lack of precise information on the manner in which a vascular meristem active in a young elongating organ is changed into a typical cambium of mature organs. On the one hand are the works dealing with early vascularization of the primary body, on the other the investigations concerned with the cambium and its derivative, secondary xylem, in woody species. Studies considering especially the transition from primary to secondary growth have hardly been attempted (66).

Thus a sure basis for reevaluation of the classification of vascular meristems and tissues is still lacking. The present writer favors, therefore, retention of the old terminology, with the understanding that the procambium may resemble the cambium in producing radial series of cells, but that certain differences in structure and development justify separate treatment of the two forms of vascular meristem and of tissues which they produce. At the same time procambium and cambium are regarded not as two distinct meristems, but as two developmental stages of the same vascular meristem.

Origin of interfascicular cambium. In many studies on interfascicular cambium the results are obscured by uncertain interpretations of primary and secondary growth and by a lack of appreciation of the high degree of plasticity of living cells as shown by their ability to produce new kinds of cells. Generally, workers were considering whether interfascicular cambium arose in a parenchyma distinct from the procambium or in a tissue more or less closely related to the procambium.

Kostytschew (120, 121) opposed the commonly used interpretation that discrete procambium bundles arose at the apex and that the cambium ring was formed through union of the fascicular cambia by segments of cambium originating in the medullary rays. He found that an interfascicular cambium arising through renewed meristematic activity in ray-parenchyma cells rarely occurred in dicotyledons. According to Kostytschew, usually a continuous procambium ring was formed and a continuous cambium ring was derived directly from the procambium. In a few plants the parts of procambium between leaf traces differentiated into parenchyma which later gave rise to interfascicular cambium. Such cambium,

however, produced only parenchyma (*Ricinus, Helianthus, Bidens, Aristolochia, Clematis,* and others). Finally, there were herbaceous plants without a closed procambium ring and without interfascicular cambium. Carstens, using arborescent gymnosperms and dicotyledons, obtained the same results as Kostytschew.

As already mentioned in connection with the discussion of the origin of procambium, Kostytschew did not clearly distinguish procambium from the less specialized parenchyma cells ("residual meristem") between procambium bundles. Furthermore, others (62, 172, 84) found, in contrast to Kostytschew, that the interfascicular cambium of *Helianthus, Ricinus, Bidens* and *Carthamus* produced vascular elements. Apparently in *Ricinus* and the Compositae Kostytschew did not follow secondary differentiation sufficiently far, or used plants of low vigor with reduced secondary growth. In vine types of stems, like *Aristolochia,* the interfascicular cambium produces parenchyma, so that the vascular strands remain discrete. Even in this type of plant, however, the inter- and intrafascicular cambia have similar potentialities, since certain sections of the fascicular cambium are constantly being given to the formation of rays like those produced by the interfascicular meristem (63), so that the original strands become split up.

Dunker agreed with Helm (102) that vascular tissues originated in a continuous meristematic ring below the apex and that some parts of this ring became procambium, others developed into ray tissue. Thus rays and procambium had the same origin and therefore the rays retained the potentiality to produce vascular tissues. Most students of growth and differentiation, however, agree that the origin of a cell does not necessarily determine its potentialities. Any living tissue, regardless of its origin, is capable of producing vascular elements. The methods of vascularization of adventitious buds—a subject reviewed in an earlier section of this paper—and the developmental history of plants showing anomalous growth (19, 100) point in this direction. Reference should also be made to the phenomena associated with establishment of vascular connections through callus in grafts (184, 50), although here resumption of meristematic activity in the form of callus production precedes vascular differentiation. Particularly instructive with regard to the ability of differentiated but living parenchyma cells to produce vascular elements are the experiments involving severance

or removal of vascular connections in mature plant organs. Moreland found that in ringed *Phaseolus* stems new conducting elements, xylem and phloem, differentiated in the protoxylem parenchyma. Freundlich observed tracheae and tracheids differentiating from spongy parenchyma cells when vascular bundles were cut in leaves of dicotyledons. These xylem elements arose either directly or after division of mesophyll cells. Kaan Albest, in similar studies on stems, observed sieve-tube differentiation, as well as xylem formation, in parenchyma outside the cut bundles. The question about the origin of interfascicular cambium is only a small part of the general problem of causal relationships in vascularization of plants. At the same time this question is also involved in the still larger problem concerning resumption of meristematic activity by so-called "mature" but living cells.

It has been common usage in the past to regard interfascicular cambium arising in ray parenchyma as secondary because it supposedly involved in its formation a return to the meristematic state of cells that have become "permanent" (63). Presently, however, the concept that cells containing normal living protoplasts are potentially meristematic is coming to be generally accepted, so that resumption of meristematic activity by a living cell is not regarded as reacquisition of a lost character, but as activation of a latent potentiality (133, 180, 100, 22, 45, 79). Therefore, the distinction between "primary" fascicular cambium and "secondary" interfascicular cambium is rapidly becoming obsolete. The present author favors complete abandonment of this distinction and thorough revision of the concept of "secondary meristems". The terms "procambium" and "cambium", "fascicular" and "interfascicular cambium" suffice for precise treatment of vascular meristems. If the terms "primary" and "secondary" be used at all, they should imply no more than that one tissue appears before the other in development of the plant body. Then it would be most practical to term the procambium a "primary vascular meristem", the cambium, both fascicular and interfascicular, a "secondary vascular meristem".

In rejecting the old idea of "primary" and "secondary meristems", Linsbauer interpreted the resumption of meristematic activity by the more or less differentiated cells as "regressive differentiation". According to this author, meristematic cells become more and more determined as they differentiate into various kinds of cells of the

plant body. This is "progressive differentiation". It involves restriction but not loss of developmental potentialities and may or may not be accompanied by obvious morphologic changes. The potentiality to produce new cells is inhibited by some unknown factors—by factors, one might add, that are based on positional correlations between the cells making up the orderly organized plant body. As long as the cells retain their living protoplasts, external or internal stimuli may remove the inhibiting factors and activate the ability of the cells to act as meristems. This return to the meristematic state is "regressive differentiation". It sets up new starting points for progressive differentiation. According to Linsbauer, progressive determination of cells may become interrupted at any stage of the process and be converted into regressive differentiation. Depending on the degree of differentiation that the cells attain before regression sets in, different degrees of dedifferentiation are involved in this process.

Linsbauer's concept of regressive differentiation is perhaps applicable to phenomena associated with regeneration and similar processes. Whether one can justifiably speak of regressive differentiation in connection with the origin of interfascicular cambium is problematical. Transformation of apical-meristem cells into procambium and cambium could be spoken of as progressive differentiation because the cambium as a meristem is less generalized and morphologically more differentiated than the apical meristem. Development of ray parenchyma from meristematic cells would also be progressive differentiation in Linsbauer's sense. Does, however, ray parenchyma become more determined and more differentiated than cambium before it gives rise to interfascicular cambium? Does this transformation of parenchyma into cambium involve regression, dedifferentiation? Apparently no answer is yet available to these questions. We obviously need further work to decide "how the organization and growth of meristems is related to the orderly 'progressive differentiation' of tissues from apical or lateral meristems" and "it seems likely that the complex phenomena of 'regeneration' or 'regressive differentiation', when they are better understood, may be expected to shed important light on the fundamental nature of meristems" (79).

In different kinds of plants, interfascicular cambium arises at different distances from shoot apices; in other words, plants differ

with respect to the timing of formation of a continuous cambium cylinder. The farther from the apex, the more pronounced is parenchymatization of the cells that eventually give rise to interfascicular cambium. As previously emphasized, procambial cells also arise at successively lower levels in the stem from cells that are progressively more and more differentiated as compared with embryonic cells at the apex. The processes of initiation of different kinds of vascular meristem are continuous and overlap each other. In a rather vaguely delimited general vascular region of a stem, increasing numbers of differentiating parenchyma cells are converted into vascular-meristem cells, some, earlier in the process, forming procambium cells, others, at lower levels, giving rise to initials of the interfascicular cambium. While this "expansion" of vascular meristem is progressing, some procambial cells are maturing into primary vascular elements. By the time interfascicular cambium appears, the procambial cells between primary xylem and phloem are already differentiated into initials of the fascicular cambium. These processes culminate in formation of a cylinder of a highly specialized and localized meristem which perpetuates itself independently of the adjacent cells and functions throughout the life of the plant.

As plants differ regarding time of origin of interfascicular cambium, so they vary with respect to comparative morphology of fascicular and interfascicular cambia. On the one hand are the vine types of stems with interfascicular cambium producing parenchyma only; on the other, the arborescent species of gymnosperms and dicotyledons in which secondary vascular tissues of fascicular and interfascicular origin are rather similar. However, even in the latter groups of plants, organization of the cambium is not entirely alike in the two regions. According to Barghoorn (15), in conifers a higher proportion of rays originate in interfascicular than in fascicular regions of the primary body. In structurally primitive dicotyledons, multiseriate rays originate in the interfascicular segments, the uniseriate in the fascicular (16).

Although roots do not have interfascicular regions in the same sense as stems, the cambium arising in the pericycle opposite the protoxylem poles is comparable to the interfascicular cambium of stems. It originates in parenchyma somewhat more differentiated than embryonic tissue at the apex; it sometimes produces only

TABLE 1

RELATIONS BETWEEN PRIMARY AND SECONDARY GROWTH IN PHANEROGAMS

Appearance of the following tissues in transsections of internodes:			Place of origin of the interfascicular cambium	Examples
Procambium	Primary vascular tissues	Secondary vascular tissues		
Continuous; leaf traces confluent with each other.	Continuous	Continuous	Entire cambial cylinder within procambium close to the shoot apex	*Oleander, Nicotiana, Veronica.* E. and MacD.* fig. 63, I; 64, D.
Discrete strands; leaf traces clearly separated from each other.	Discrete strands	Continuous	In more or less young ray parenchyma cells more or less close to the shoot apex	Coniferae; most of the arborescent dicotyledons; herbaceous dicotyledons with considerable secondary growth; *Salix, Sambucus, Helianthus, Pelargonium, Ricinus.* E. and MacD.* fig. 63, H; 64, F.
"	"	Discrete strands; interfascicular cambium forming parenchyma	In ray parenchyma somewhat removed from the shoot apex	*Aristolochia* and other woody vines. E. and MacD.* fig. 64, G.
"	"	Discrete strands	No interfascicular cambium	Reduced dicotyledonous herbs with little secondary growth. E. and MacD.* fig. 64, I.
"	"	None	No cambium	Reduced dicotyledonous herbs without secondary growth, as *Ranunculus;* herbaceous monocotyledons.

* Eames and MacDaniels, 1925.

parenchyma; if it produces secondary xylem, the latter may show the same special ray characteristics as secondary xylem of interfascicular origin in stems (16).

Table 1 serves to summarize the different possibilities in origin of interfascicular cambium and in organization of vascular systems in stems of angiosperms and gymnosperms. The first three columns indicate the nature of the vascular skeleton, in primary and secondary states, as seen in transverse sections of internodes; they show whether the vascular tissues appear in discrete strands or form a continuous cylinder. The procambium is characterized as continuous when the traces are early confluent with each other. Procambium of this type is initiated as in plants with discrete bundles, that is, the procambial divisions, when viewed in transsections, begin in median positions beneath the emerging leaf primordia; however, these divisions quickly spread laterally so that the individual traces come in contact with each other. Primary xylem and phloem also appear first in the median positions of the traces, then differentiate laterally and eventually appear in a continuous ring. In other words, the traces are rather indistinct. Most phanerogams have discrete strands in the primary vascular body, but the tangential extent of "medullary" rays varies greatly. It is conceivable that in some plants interfascicular segments, while still in meristematic state, could be interpreted as procambium even though these segments would not give rise to primary vascular tissues but would form directly the interfascicular cambium.

The table is not presumed to be complete with regard to examples cited for different types of vascular systems. It is offered merely as a working basis for further comparative studies designed to elucidate the relation between primary and secondary growth of vascular tissues.

Relation between primary and secondary growth in monocotyledons. Generally, the vascular system of the primary body of monocotyledons is composed entirely of leaf traces. The earlier appearing traces of each leaf, which are also usually the larger, differentiate near the center of the stem in their upper parts and near the periphery in their lower parts (traces ending at *A, B* and *C* in Fig. 11). Subsequently appearing traces, commonly smaller than the earlier ones, differentiate successively nearer the periphery of the stem (traces ending at *a, b* and *c* in Fig. 11).

In certain arborescent and herbaceous monocotyledons, particularly in the Liliflorae, the vascular system is augmented through a special kind of secondary growth resulting from activity of an extrafascicular meristematic region commonly referred to as the "cambium" (63, 43). The latter occurs near the periphery of the stem and produces toward the interior discrete vascular bundles and parenchyma. The bundles and parenchyma cells are arranged in radial rows because they originate in a tangentially dividing meristem (19, 43). Some parenchyma, the "secondary cortex", is produced toward the periphery. The secondary vascular bundles are connected with the leaf traces composing the primary vascular system but are themselves not regarded as traces (19, 192, 193).

Primary vascular bundles arise by a process very similar to that involved in the production of secondary tissues. Monocotyledons are characterized by a thickening growth of primary nature which occurs through the activity of a cambium-like lateral meristem (178, 179, 104, 12; and others). This meristem becomes first evident beneath the young or youngest leaf bases and remains active to variable distances downward, depending on the species. It gives rise to the bulk of the stem tissues, including the leaf traces. In transsections the thickening meristem occupies a ring-like zone and in it tangential divisions cut off cells toward the interior of the axis. In a three-dimensional aspect this primary thickening meristem has the shape of an inverted cone with the apex removed, or it is a flat zone, or a concave bowl-shaped region (*e.g.*, 12). In the portion proximal to the apex the meristem produces the parts of the traces that occur nearer the center of the axis; farther from the apex the meristem forms the peripheral strands. Judging by the work of Baranetzky and Ball the very first bundles near the apex of the stem may be produced not by the thickening ring but directly from derivatives of the shoot apex.

Many early workers described an annular meristematic zone in shoot apices of monocotyledons (116, 174, 140, 168, 19, 13) and variously called it "formative ring", "cambium ring" and "thickening ring". Schoute (178) referred to it simply as "cambium". Helm (104) has suggested that the meristem described by these workers refers, at least in part, to the primary thickening meristem.

As was mentioned in the section on the relation between procambium and apical meristem of stems, workers have described in

phanerogams a special meristematic region which appears beneath the promeristem and is later concerned with formation of procambium. Bouygues (27) and Kaplan (114, 115) specifically mentioned monocotyledons as having such a region, but did not relate it to the primary thickening meristem of other workers. Helm (104), however, suggested that the "meristem ring" described by him as the precursor of the vascular region in dicotyledons (102) was similar, in certain respects, to the primary thickening meristem of monocotyledons. Both caused thickening of the axis—in dicotyledons the meristem ring brought this about by first giving rise to the cambium—and both contributed vascular tissues to the axis.

The older workers (116, 174, 140) considered the thickening meristem of monocotyledons as continuous with the promeristem of the apex. Helm (102, 104) held a similar view regarding both the meristem ring of dicotyledons and the primary thickening meristem of monocotyledons. With reference to the latter, Helm emphasized that this meristem arose from "fully meristematic cells" and was directly continuous with the "Urmeristem" of the apex. In contrast, Ball found that in palms the primary thickening meristem and the shoot apex were somewhat independent of each other in their activities. According to Ball, the thickening meristem arose beneath very young or somewhat older leaf primordia so that possibly the formation of this meristem had some aspects of regressive differentiation. (In this connection Ball erroneously ascribed to Helm (104) the same viewpoint.)

Many workers were concerned with the relation between primary thickening growth and secondary growth in monocotyledons. According to Petersen, monocotyledons with and without secondary growth are not sharply distinguished from each other. Some plants have no specific meristem concerned with growth in thickness (Orchidaceae), others have such meristem beneath the apex but of limited duration (Scitaminaceae); in still others the meristem functions longer (Bromeliaceae, palms) and may be continuous from the top to the base of the plant (*Agave*); finally, the meristem may arise at a considerable distance from the apex and function indefinitely (*Dracaena*). These meristems, according to Petersen, may show different degrees of orderliness in cell arrangement.

Guillaud and Scott and Brebner regarded secondary growth as entirely independent of the primary, since, according to their find-

ings, this growth began some time after completion of the primary body and the meristem concerned arose from mature parenchyma cells. According to De Bary (19), in certain woody monocotyledons (*Yucca, Calodracon, Aloe, Beaucarnea*) the cambium producing secondary thickening arose immediately below the apex before primary growth was completed but in most Dracaeneae it first appeared in regions of considerable age. Skutch stated that the cambium-like meristem in the banana bulb which arose close behind the apex from immature cortical cells quickly exhausted itself but was succeeded in turn by other meristematic layers which also arose in the cortex and followed a similar history. (Helm (104) found only primary growth in *Musa chinensis*.)

In contrast to the above workers, Lindinger considered that in all monocotyledons primary and secondary thickening growth were continuous, even in the Dracaeneae. If the latter appeared to have an interruption between "primary" and "secondary" meristem this occurred because the meristem after completion of primary growth remained quiescent for a time but later resumed activity to produce secondary tissues. Chouard expressed a similar view. According to this worker, "secondary" formations in *Yucca, Dracaena* and other woody monocotyledons result from a persistent activity, perhaps an augmented and regularized activity, of a meristematic cylinder directly continuous with the apical meristem. In Chouard's opinion the method of growth of *Scilla* bulbs is not fundamentally different from that of stems and branches in Bromeliaceae, *Yucca* or palms.

Primary thickening meristem is usually interpreted as an "Etagenmeristem", "Etagencambium" or "tiered" meristem (131, 177, 12) in which there is no constant initial layer, but, in which different cells continuously succeed each other in the production of new tissues. The meristem causing secondary growth, according to Schoute (177), also begins as an "Etagenmeristem" but may become an "Initialenmeristem" in older stems.

According to many workers (163, 192, 182, 9, 43), the secondary bundles of monocotyledonous stems and often also the outer or peripheral leaf traces lack protoxylem. The latter appears to be largely confined to the inner primary strands which differentiate before the stem completes its growth in length.

From the above review it seems that regardless of the place of

origin of secondary thickening ring or cambium, whether it arises in continuity with primary thickening meristem or separately from it, monocotyledons with and without secondary growth show a common plan of development. Vascular bundles arise within a tissue formed by a peripheral cambium-like meristem. The earliest bundles develop before the stem elongates and appear nearer the center of the axis in their upper parts and nearer the periphery in their lower parts (Fig. 11). After elongation, strands mature near the periphery of the stem. A limited number of such strands develop in monocotyledons without secondary growth; but their numbers may be great and indefinite if they arise chiefly as a result of secondary thickening. Primary bundles are leaf traces or their direct prolongations. Secondary strands are connected with the traces but are themselves not regarded as such.

Monocotyledons differ strikingly from dicotyledons in the manner of secondary growth: in the former, complete "closed" bundles are produced by the meristem in one direction; in the latter, xylem and phloem appear on the two opposite sides of the meristem concerned with their formation. As Strasburger (192) pointed out, however, there is a fundamental similarity between the two groups of plants regarding the relation between primary and secondary growth. In both, secondary tissues differentiate higher and higher up the stem and continuously make connection with the traces of leaves appearing at successively higher levels. In both there is no sharp demarcation between primary and secondary growth.

According to Dauphiné (58), the resemblance between monocotyledons and dicotyledons with regard to the general plan of development of the vascular system is particularly apparent if the former are compared with those dicotyledons that show anomalous growth of the chenopodiaceous type, in which successive layers of secondary bundles and interfascicular parenchyma are produced centrifugally from the original ring of primary bundles. De Vries found that in the fleshy storage organ of the beet the leaf traces were connected with the successive anomalous rings, the older leaves with the inner rings, the younger with the outer ones. Alexandrov (1) interpreted the vascular strands in these rings as leaf traces and suggested that the anomalous portion of the beet root was in reality stem-like in nature. Each leaf in the beet plant is connected with more than one ring; the larger, earlier ones continue into rings that

occur deeper in the root than the rings which are connected with the smaller later traces. The similarity with the vascular system of monocotyledons is obvious.

Interpretation of continued thickening of axes in certain monocotyledons as secondary growth is in keeping with the suggested definitions of primary and secondary growth given in preceding parts of this paper. Secondary growth in monocotyledons is not necessarily clearly separated from the primary but constitutes an addition to a primary body which is complete in itself. Secondary tissues also differ from primary in the manner of growth and in their structure (43). The terminology regarding the meristems involved in the growth of the monocotyledonous axis, however, is in need of revision for which a sure basis is still lacking. In primary growth the cambium-like "primary thickening meristem" gives rise to cells, some of which by further subdivision form the "procambium" strands. In secondary growth a secondary thickening meristem, or "cambium", closely related in nature and activity to the primary thickening meristem, also gives rise to distinct vascular strands. In the immature state these strands have been referred to as "procambium" (117), "desmogen" (43) or "secondary desmogen" (181). If the term "cambium" is retained for the meristem producing secondary tissues in monocotyledons, then application of the term "procambium" to the strands resulting from the cambium is incongruous. "Desmogen", by its original definition, refers to the same structure as "procambium", that is, to the meristematic tissue differentiating into primary vascular strands, and is, therefore, equally unsuitable as "procambium" for designation of the immature secondary vascular strands.

Concepts of protoxylem and metaxylem. In formulating their concepts of primary and secondary vascular tissues the early workers recognized differences between successive formations in the primary xylem. Eventually the earliest xylem became known as protoxylem, the rest of the primary xylem as metaxylem (*e.g.*, 63, 100, 108). As Bugnon (32) has pointed out, the terms "protoxylem" and "metaxylem" have been considerably modified since they were first conceived. Moreover, controversies arose concerning the exact meaning of these terms, so that at present the concepts of protoxylem and metaxylem are rather uncertain.

For details on the origin and evolution of the terms "protoxylem"

and "metaxylem", the reader is referred to the excellent review of this topic by Bugnon (32). Here it will suffice to bring out the main points in the development of the concepts of these tissues.

The term "protoxylem" was introduced by Russow (163) to designate the xylem elements that appeared at the beginning of vascular differentiation and occupied a characteristic position in the primary vascular skeleton. The location of these protoxylem cells definitely marked the pattern of differentiation which was followed by subsequently appearing primary xylem elements. This pattern varied, depending on the plant group or type of organ so that plants and organs could be classified on the basis of the order of xylem development, whether exarch, mesarch or endarch. The concept of protoxylem proved very useful with regard to such a classification in both cryptogams and phanerogams. In the latter Russow noted, however, that certain bundles lacked protoxylem, although they arose from procambium. These were bundles that appeared somewhat late during primary differentiation.

The histologic structure was of secondary importance in Russow's concept of protoxylem. He mentioned that protoxylem elements were commonly of small diameter, but that their secondary walls could be of any type known in the xylem—annular, spiral, scalariform, reticulate, pitted—and, inversely, elements other than those of the protoxylem, primary or secondary, could have the same kind of wall thickenings as the protoxylem. Thus in roots of gymnosperms and the Gramineae rings and even spirals appeared to be lacking. On the other hand, many Crassulaceae showed spiral thickenings in vessels of the secondary xylem. Usually, however, the protoxylem contained annular and spiral tracheal elements and Russow thought that these kinds of xylem cells were also phylogenetically the most primitive.

Because of the inconstancy in histologic details the precise delimitation of Russow's "protoxylem" in a given plant was difficult, or even impossible, if transition from the first to the last primary xylem was very gradual. As Bugnon (32) has pointed out, Russow's "protoxylem" was conceived entirely from the ontogenetic viewpoint: the protoxylem was a starting point of ligneous differentiation. It was important to know whree the protoxylem began and not where it ended.

Thus Russow introduced a convenient term to designate the

initial xylem in the plant body—the "xylem pole" of the French workers. Moreover, this term played an important rôle in the evolution of the concepts of exarch, mesarch and endarch xylem (32).

Van Tieghem (199) erroneously applied Russow's term "protoxylem" to all of the centripetal xylem of roots and coined the term "metaxylem" for the centrifugal xylem elements that occupied, in these roots, the same position as the secondary elements but were not yet derived from the cambium. Subsequent workers adopted the term "metaxylem" but changed its original sense. Gradually, through the writings of students in fossil botany (See 32), "metaxylem" began to be employed in opposition to "protoxylem", denoting all the primary xylem that differentiated after the protoxylem.

The original meaning of protoxylem was modified when workers began to distinguish between protoxylem and metaxylem on the basis of the wall sculpture of the tracheal elements (See 32). Eventually the tendency to ascribe to protoxylem and metaxylem a definite wall morphology became prevalent and it influenced the formulation of concepts of primary xylem by writers of modern reference works. In some of these the scalariform and reticulate elements were classified as metaxylem (100), in others the reticulate and pitted (63, 79). According to the International Association of Wood Anatomists (108), metaxylem contains pitted tracheary elements, but they include among the pitted the scalariform elements also.

The wall sculpture of protoxylem elements was early brought into a relation to the fact that the first xylem elements developed in organs which were still rapidly growing in length. Russow (164), for example, speculated that annular and spiral cells were particularly suitable for rapidly elongating plant parts because they required small amounts of material and energy for their formation and could develop quickly. Then the idea was evolved that the wall markings of the protoxylem were a result of an adaptation to stretching which these elements normally underwent after maturation (*e.g.,* 63); that they were an expression of a structural and physiological correlation (100).

Thus originally the distinction between protoxylem and metaxylem was made with regard to the relative time of appearance of these two tissues, but later the consideration of morphologic differences was superimposed over the original concept. A further com-

plication was introduced into the problem by the efforts of certain workers to revise the concepts of primary and secondary vascular tissues. As previously reviewed, frequently all the xylem, primary and secondary, arises from a radially seriated meristem. Many workers therefore preferred to consider all such xylem as secondary (*e.g.*, 153, 154, 42).

Incidentally, a recent study (188) supports the idea that the type of wall thickening in primary xylem is determined by the extent of elongation of the surrounding tissue. *Vicia faba* roots from seeds irradiated with soft x-rays showed decreasing total elongation as increasing doses of x-rays were employed. Instead of the normal sequence of annular, spiral, scalariform and pitted elements formed at successively lower levels of the root, the roots in which growth had been slowed down showed a tendency to omit the earlier types of xylem elements. When the decline of growth was the greatest the first elements to differentiate near the apex had pitted secondary walls.

Bugnon (32) and Frey-Wyssling have made a beginning of a very necessary reevaluation of protoxylem and metaxylem concepts. Both these workers favor abandonment of delimitation of these two tissues on the basis of the wall sculpture of their elements and advocate reintroduction of the ontogenetic aspect into the classification. Bugnon proposes to use "protoxylem" in the original sense as indicating the center or pole of ligneous differentiation; "metaxylem", as primary xylem elements succeeding the protoxylem. He adds that in primitive xylem (*e.g., Rhynia*) separation into protoxylem and metaxylem cannot be made on a morphological basis but in more advanced plants various degrees of distinction exist between the two tissues, the protoxylem usually having elements of small diameters. In plants with secondary growth evolution has been progressing toward a reduction in the amount of primary xylem until nothing is left but protoxylem, according to Bugnon. Even if all vascular elements are formed by a cambium, he thinks the narrow elements appearing at the poles of xylem differentiation should be termed "protoxylem".

Frey-Wyssling used a new method of approach to the classification of xylem—a method foreshadowed in Bailey's studies on lengths of tracheal elements in xylem of different ages. Frey-Wyssling considered the developmental history of different parts of the xylem

in relation to growth of the whole organ. According to this worker, recently matured protoxylem elements are very short, since their differentiation is completed before growth in length of the organ sets in. By such growth the protoxylem elements are stretched, torn and destroyed. Frey-Wyssling points out that in the literature these elements are most often represented as being very long, because they are shown after they had been subjected to stretching. Metaxylem cells arise during growth in length and show intensive apical growth. Frey-Wyssling states that when they mature, metaxylem elements are much longer than protoxylem cells in a corresponding stage of differentiation and that successive layers of metaxylem show progressively longer elements. He finds, however, differences in structure of metaxylem in different groups of plants. In stems of monocotyledons and dicotyledons with reduced secondary growth and generally in roots the last metaxylem elements have large diameters, show little apical growth, and develop pitted secondary walls. In arborescent dicotyledons short pitted tracheal elements appear only with the onset of secondary growth, the metaxylem elements all being long, with spiral secondary thickenings. In gymnosperms having long fusiform cambial initials secondary growth continues with the production of long slender tracheids begun during metaxylem formation. This, incidentally, does not agree with the results obtained by Bailey who found a sudden drop in length of tracheal elements at the start of secondary growth not only in dicotyledons but also in gymnosperms.

According to Frey-Wyssling, the protoxylem consists only of water-conducting elements. Secondary xylem has a triple function, that of conduction, support and storage, and accordingly shows a highly complex structure. The metaxylem occupies an intermediate position between protoxylem and secondary xylem in both function and structure.

The present writer favors the reinterpretation of the concepts of protoxylem, metaxylem and secondary xylem on an ontogenetic basis and in relation to development of the organ as a whole. Further studies on a wide variety of materials are, of course, needed to test the usefulness of such an interpretation. Therefore the following formulation of the concepts is offered in a tentative way and refers only to the gymnosperms and angiosperms. Certain ideas of Bugnon and Frey-Wyssling have been used in this formulation, but

were partly modified in accordance with the writer's own observations.

Using the previously suggested broad definitions of procambium and cambium as two developmental phases of the vascular meristem, primary xylem is regarded as derived from procambium in connection with differentiation of the other primary tissue zones. This phase of development is typically characterized by growth in length of the entire organ. After this growth terminates, cambial activity and production of secondary vascular tissues set in. Although primary and secondary tissues greatly differ from each other in development and morphology, the terms "primary" and "secondary" are used only in the sense that one tissue appears before the other. Within the primary xylem the earliest part—the "protoxylem"—lays the foundation of the pattern of differentiation of the primary xylem. In roots it marks the poles from which the rest of the primary xylem, the "metaxylem", matures centripetally; in stems it appears on the inner margin of leaf traces. Protoxylem is most abundant in those traces or parts of them that are completely differentiated while the organ is undergoing its major elongation (154). Protoxylem, as well as all the other xylem, of roots differentiates in continuity with the xylem at the base of the organ; in stems, protoxylem first appears in the trace near the base of the leaf, or in the leaf proper, and from here differentiates acropetally into the elongating leaf and basipetally into the axis until it unites with the mature xylem of the traces of older leaves (Fig. 12). Since protoxylem matures before the axis completes elongation, it is stretched. Depending on the degree of this elongation, protoxylem elements may be torn and destroyed, more or less completely, as the primary body matures. Annular and spiral secondary thickenings commonly occur in the protoxylem of much elongating organs. Metaxylem begins to differentiate during elongation of the organ, but matures mostly after this growth is completed. In its mature state metaxylem is therefore not affected by stretching. Metaxylem cells, however, commonly elongate very much before their secondary walls are deposited, so that the mature elements are very long. The last of metaxylem elements in roots and stems with little or no secondary growth probably differentiate after elongation ceases and therefore may remain short (81). The sculpture of secondary walls of the metaxylem may vary from spiral to pitted. Whether or not

metaxylem in its development within the leaf trace follows the same direction as protoxylem remains to be determined.

Further studies are necessary to determine whether protoxylem and metaxylem can be sharply delimited. In elongating organs Frey-Wyssling recognizes as protoxylem only the elements that mature before growth in length sets in and which are stretched and destroyed during elongation. Some anomalous plants or organs do not elongate (21). In such instances the protoxylem would not be stretched, as Frey-Wyssling himself has indicated, and the metaxylem, as a tissue differentiating during elongation, would not be present. It is highly probable that the protoxylem and metaxylem of plant organs that grow in length merge gradually into one another; some xylem elements mature early and undergo complete destruction; others, conceivably, are stretched in mature state without complete destruction; finally, some elongate only in immature condition.

Recently Popham (151) suggested abandoning the terms "protoxylem" and "metaxylem" because "in the differentiation of xylem cells, the size, location, time of enlargement, time of secondary wall lignification, time of differentiation, and the pattern of the secondary wall do not always bear a specific or constant relationship to the kind of origin, whether primary or secondary". The causes of confused usage of these terms have been analyzed in the preceding paragraphs and sections of this review and a way to reduce this confusion has been shown. In the present writer's opinion the concepts of protoxylem, metaxylem and secondary xylem, when used as defined in this review, give a dynamic picture of xylem ontogeny in a plant or an organ as a whole and elucidate the relation of the different phases of vascular differentiation to development of the organ in which these tissues occur.

Concepts of protophloem and metaphloem. The terms "protophloem" and "metaphloem" evolved in relation to the development of xylem terminology. Russow (163), in naming protophloem, stated that morphogenetically this tissue corresponded to protoxylem: it arose in the procambium and appeared before all other phloem elements. He recognized sieve tubes in the protophloem and observed that this tissue had mature elements before the protoxylem. Russow also noted crushing of the protophloem in late stages of primary organ development. This author's observations were subsequently confirmed by many other workers (67).

When Van Tieghem first employed the term "metaxylem" he suggested that the term "metaphloem" be used for the part of the phloem that differentiated at the same time as the metaxylem. But he also pointed out that no clear distinction existed between different parts of the phloem so that it was hardly necessary to use two terms for this tissue. Eventually, however, the terms "protophloem" and "metaphloem" became fixed in a similar relation to each other as the two corresponding terms for the primary xylem. The morphology of walls, obviously, did not become involved in the definition of the two parts of primary phloem, but some workers introduced the erroneous concept that sieve tubes were absent from protophloem (63).

Esau (65, 66, 68, 69) made an effort to distinguish between protophloem, metaphloem and secondary phloem of dicotyledonous stems and roots on the basis of ontogeny and emphasized the early appearance and more or less complete destruction of protophloem in elongating organs. The metaphloem was interpreted as a tissue maturing largely toward the end of growth in length of the primary body. Secondary phloem arose from the vascular meristem organized as a cambium in the plant body that had ceased to elongate.

Protophloem, similarly to protoxylem, fixes the pattern of differentiation of primary phloem: it marks the phloem poles in the root which alternate with the protoxylem poles; in stems it appears in the leaf traces, on the outer margins of procambium strands. Acropetal differentiation of protophloem is probably typical of roots and stems of phanerogams.

Concept of pericycle. Recognition of protophloem is particularly important with regard to the concept of pericycle in vascular plants. The term "pericycle" was introduced by van Tieghem (197) to denote the ring of sclerenchyma and the subjacent parenchyma outside the vascular bundles of *Cucurbita* stems, that is, the stem region enclosed between endodermis and vascular tissues. On the basis of extensive comparative studies, Morot concluded that a pericycle in the sense of van Tieghem occurred in roots and stems of practically all plants and that it was derived from the same fundamental meristem as rays and pith. In roots the pericycle is usually parenchymatous, at least in the primary state. The pericycle of stems varies in thickness and composition. Frequently it contains fibers, either in continuous layers or as discrete strands. The con-

cept of the pericycle was originally developed with regard to the mature stem structure (198); its ontogenetic relation to other tissues was of secondary importance.

D'Arbaumont contested Morot's viewpoint because ontogenetic studies on many woody and herbaceous species indicated to him that mostly the pericycle was formed by procambium and was merely a specialized part of the phloem. In the Cucurbitaceae the pericycle arose from a formative tissue similar to procambium but separated from the vascular zone by ground parenchyma. Then Léger, clearly understanding the development and old-age metamorphosis of the primary phloem, furnished conclusive proof that in most plants the so-called "pericycle" was not a distinct region but constituted the earliest part of the primary phloem in which sieve tubes and companion cells had been obliterated. Léger considered a very large number of plants in 32 different families, including phanerogams and cryptogams.

Among the subsequent workers, Gidon reported absence of pericycle in the Nyctaginaceae. Pitard, after examining stems of 104 families of dicotyledons, concluded that the pericycle did not exist as an autonomous zone. Esau (65, 66) was able to confirm Léger's interpretation by detailed developmental studies on the origin of the bundle cap in vascular bundles of celery and of the fibrous layer on the periphery of tobacco phloem. Both these structures originated in the protophloem region. The pericycle of roots is also closely related to the vascular tissues, as has been shown in the part of this review dealing with primary root structure.

Despite its high quality, Léger's work found, in general, little recognition; instead, Morot's interpretation, that a pericycle was universally present as a distinct region in stems and roots and that it arose from the same fundamental meristem as the medullary rays and pith, largely came to dominate our concept of the pericycle as a layer originally independent of the vascular tissues. Studies on the origin and ontogeny of primary vascular tissues must eventually lead to a reinterpretation of the pericycle concept.

CONCLUSION

In conclusion it seems appropriate to indicate some of the basic concepts that have determined the writer's approach in the present evaluation of terms, concepts and interpretations. Morphological

categories and terms are tools that we need to describe our observations. If these terms and categories are conceived narrowly and on the basis of a static picture of plant structure, and if, in addition, they are used injudiciously, they become obstructions that stand between us and the facts revealed by pure observation. At their best, terms and categories are inadequate to express fully the common tendency of living organisms to intergrade in structure and function with other related organisms and to produce, within themselves, transitional types between the different categories of cells, tissues or organs. But we need these tools, we require a language to describe our observations, and we wish this language to be uniform and clearly understood. In view of the nature of the subject, our concepts, terms and categories must be conceived broadly and with an emphasis on the dynamic aspects of the organization of plants. Living organisms are not conglomerations of separable parts, they are not merely cell networks, but are aggregations of living elements intimately associated with other elements adjacent to them in time and space.

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Metabolic Phenomena in Plants Associated with Virus Infection	F. L. WYND *University of Illinois*
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Plant Life and the Law of Man. IV. Barberry, Currant and Gooseberry, and Cedar Control	E. H. FULLING *The Botanical Review*
The Cuticle in Angiosperms	J. H. PRIESTLEY *University of Leeds*
Lichens—Their Biological and Economic Significance	G. A. PEREZ-LLANO *Harvard University*
Root-rots of Some Non-cereal Crops	G. H. BERKELEY *Dominion Laboratory of Plant Pathology*

Articles arranged for most recently

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Plant Oils	J. B. MCNAIR *Field Museum, Chicago*
Paleobotanical Taxonomy	H. L. MASON *University of California*
Development of the Madro-Tertiary Flora	D. I. AXELROD *University of California*

Articles in course of preparation

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